LAMPETRA (ENTOSPHENUS) LETHOPHAGA, NEW SPECIES, THE NONPARASITIC DERIVATIVE OF THE PACIFIC LAMPREY

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ABSTRACT.—The Pacific lamprey, *Lampetra (Entosphenus) tridentata,* is now shown to agree with most parasitic species of the Petromyzoniformes in having evolved into a nonparasitic derivative, *L. (E.) lethophaga.* Although the parasitic form ranges widely, from central Baja California around the North Pacific periphery to southern Japan, varying greatly in adult size, the dwarfed nonparasitic form seems to be confined to the contiguous drainage basins of the Pit River (a Sacramento River headwater) in northeastern California, both above and below the Pit River Falls, and to the upper Klamath River system in south-central Oregon. These two drainage basins harbor additional endemic fishes, and have certain other faunal features in common. The distributions of the three nonparasitic lampreys in the drainage basins around the North Pacific appear to be complementary.

L. lethophaga contrasts rather sharply with the dwarfed, probably resident types of *L. tridentata* in the Klamath system, as well as with the large, sea-run populations. However, a specimen from Willow Creek in the Lost River system of Oregon is possibly intermediate between *L. lethophaga* and the dwarf parasitic types in the Klamath River system; and a parasitic form of the same group, of Miller Lake, in a disjunct section of the Klamath River system, is reported to be even more dwarfed than *L. lethophaga.* Some intergradation between the parasitic and nonparasitic stocks is not excluded.

The dentition of the nonparasitic form exhibits features both of reduction and of increased individual variation, probably along with some geographical differentiation.

Like other lampreys, the new species no doubt exists for several years in the larval (ammocete) stage before metamorphosing in the autumn. The gonads ripen as the gut atrophies. The dwarf adults after overwintering appear on circumstantial evidence either (1) to undergo the typical nuptial metamorphosis to spawn in the following spring, or (2) to attain maturity neotenically while retaining the prenuptial state of pigmentation and body form, and to spawn over the summer months, or even after overwintering again.

There are indications that lamprey species are subject to regional diversity, and that some of the speciation has been of a mosaic type.

RESUMEN.—Se demuestra que la lamprea del Pacífico, *Lampetra (Entosphenus) tridentata* concuerda en su evolución con la mayor parte de las especies parasíticas de Petromyzoniformes, produciendo un derivado no parasítico, *L. (E.) lethophaga.* Las formas parásitas presentan una amplia distribución geográfica, extendiéndose a lo largo de la zona periférica del Pacífico Norte, desde la parte central de Baja California hasta la zona meridional del Japón. Los adultos de estas formas ofrecen una gran variación de tallas. Las formas enanas libres, no parasíticas, están al parecer confinadas a las cuencas fluviales contiguas del río Pit (uno de los tributarios de la parte alta del río Sacramento) en la zona nordeste de California, a ambos lados de las cataratas del río Pit, y en la parte alta del sistema del río Klamath en la zona centro-meridional de Oregón. Estas dos cuencas fluviales albergan también otros peces endémicos, presentando así mismo otras características faunísticas comunes. Las tres lampreas no parasíticas que habitan las cuencas fluviales que bordean el Pacífico Norte, presentan al parecer una distribución complementaria.

L. lethophaga contrasta notablemente con las formas enanas, probablemente tipos residentes de *L. tridentata* en la red fluvial del Klamath, así como también con las especies de talla grande correspondientes a poblaciones oceánicas. Sin embargo, un ejemplar procedente de Willow Creek, en la red fluvial del río Lost, en Oregón, es posiblemente una forma intermedia entre *L. lethophaga* y los tipos parasíticos y enanos del sistema del río Klamath. Una forma parasítica de este mismo grupo aparece en el lago Miller (sección disyuntiva de la red fluvial del río Klamath). Se ha establecido ya, que dicha forma es aun más pequeña que *L. lethophaga.* Desde luego no puede excluirse la posibilidad de que exista una intergraduación entre las poblaciones parásitas y libres (no parasíticas).

Las formas libres presentan variaciones individuales de reducción o de incremento en la dentición, características probablemente relacionadas con otras diferencias geográficas.

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Al igual que sucede en otras lampreas, esta nueva especie permanece induablemente durante varios años en la fase larval (amoceto) antes de llegar a la metamorfosis, que tiene lugar en el otoño. Al madurar las gónadas, el tubo digestivo se atrofia. Los adultos enanos despues de pasar el invierno, evidencian cualquiera de las siguientes circunstancias: 1) que pasan la metamorfosis nupcial típica para así desovar en la primavera siguiente, o 2) alcanzan una madurez neoténica, es decir, retienen la pigmentación y forma del cuerpo de la fase prenupcial, desovando entonces durante los meses de verano, o aún mas tarde, después de pasado el invierno.

Las observaciones obtenidas indican que las especies de lampreas presentan diversidad regional, y en algunos casos la especiación corresponde al tipo de mosaico.

Although I discovered a dwarfed, nonparasitic derivative of the Pacific lamprey, *Lampetra (Entosphenus) tridentata* (Richardson) in 1934, in the Pit River system of northern California and in the upper Klamath River system in southern Oregon, and although it has been distinguished by Bond (1961: 14) in key form from *L. tridentata*, from the same river systems, it has not yet been assigned a species-group name. Bond merely designated it "Klamath brook lamprey, *Lampetra* sp." With the particular need of making the name and the status of this form available for a forthcoming treatment of the distribution, phylogeny, and taxonomy of lampreys (Hubbs and Potter, in press), it is now belatedly made known as:

PIT-KLAMATH BROOK LAMPREY

Lampetra (Entosphenus) lethophaga, new species

Entosphenus tridentatus (misidentification).— Rutter, 1908: 120 (material listed from "South Fork Pitt River" only).

Lampetra planeri (misidentification).— Hubbs, 1925: 594 (size of recently transformed specimen from "North Fork of Pitt River").

Lampetra sp.— Bond, 1961: 14 ("Klamath brook lamprey"; "Klamath and Pit River systems").

Holotype, U. Mich. Mus. Zool. 130648, and paratypes, UMMZ 130649, from source of Fall River, a tributary to Pit River, in Shasta County, California (as specified under Location 2, below).

This species is illustrated in Figures 1, 2 A-B, and 6; its range and habitat in Figures 3 and 4; its size in Figure 8. Figures 2 C-D, 3, 5, 7, and 8 pertain in part or *in toto* to related forms.

Diagnosis.— The following diagnosis largely follows the sequence of characters utilized by Hubbs and Potter (in press) in their analysis of the lampreys of the world.

A petromyzonid lamprey agreeing with *Lampetra (sensu lato)* in having: the extraoral teeth not in regular alate rows, the lateral and posterior fields of disc essentially toothless between circumorals and marginals, the teeth of the anterior field few and scattered, none of the teeth villiform, the supraoral markedly dilated, the anterior circumorals normally 5, the total anterior and lateral circumorals usually 13, and the lateral circumorals more or less dilated. Agreeing with subgenera *Lethenteron* and *Entosphenus* in having the laterals connected by the posterior circumorals, and agreeing with *Entosphenus* in having 4 lateral circumorals on each side, one or more outer posterior circumorals often bifid, the supraoral often with a median cusp, the transverse lingual lamina almost rectilinear and with median cusp not strongly enlarged, and the marginals and posterior circumorals often in an irregular file. Differing from the complex now passing as *Lampetra tridentata* in being nonparasitic (not feeding or growing after the fall metamorphosis, but developing the gonads as the gut atrophies prior to spawning in the next spring or summer, or even later, and then dying), and in being much reduced in size at maturity (less than 170 mm), and in some places (including the type locality) breeding in prenuptial coloration and body form;

also differing from *L. tridentata* in having the mouth small (disc length less than 5 percent of total length) and usually much puckered, the median cusp of supraoral often weak or absent, the cusps on the lateral circumorals often reduced by 1 on any of the four teeth from the formula 2–3–3–2, the posterior circumorals reduced in number (9 to 15), and the anterior intermediate disc teeth, between anterior circumorals and marginals, very few (only 4 in specimen shown for dentition as Figure 6).

MATERIAL

The considerable amount of material (Table 1) referred to *Lampetra lethophaga* has come from various places in the Pit River system of northeastern California and in the Klamath River system in south-central Oregon (Figure 3). The available information on the habitats at the 11 localities, 5 in the Pit system and 6 in the Klamath, and on the associated fish species and the circumstances of the collecting, is detailed because of the bearing that this information has on the interpretation of the distribution, environment, variation, and life history of the species. The localities are listed separately for the Pit and Klamath systems, in each basin from upstream downward.

Material used in this study has been deposited in the following institutions: CAS, California Academy of Sciences; CU, Cornell University; OS, Oregon State University; SIO, Scripps Institution of Oceanography; SU, Stanford University (material now transferred to California Academy of Sciences); UMMZ, University of Michigan Museum of Zoology; USNM, United States National Museum.

LOCATIONS IN PIT RIVER SYSTEM, NORTHERN CALIFORNIA

1. North Fork of Pit (formerly "Pitt") River at mouth of Joseph Creek, near Alturas, Modoc County, collected by Cloudsley Rutter and Fred M. Chamberlain, September 4, 1898. These data are taken from the label, but the specimens may have come instead from the South Fork of Pit River, for Rutter (1908: 120) failed to list the North Fork among the collections entered for "*Entosphenus tridentatus,*" but did include it for "South Fork Pitt River (South Fork P.O., Jesse Valley"); also collected by Rutter and Chamberlain(the location of "Jess Valley," as now mapped at altitude of ca. 1585 m is located by a question mark on the distributional map, Figure 3). In any event, it seems almost certain that Rutter's record was based on *L. lethophaga*.

The 2 specimens (UMMZ 55316) making up this collection, received from Stanford University, comprise a female 142 mm long, in early stage of transformation, with eggs few enough to indicate a nonparasitic form, and an ammocete 105 mm long, with minute ova. The female was recorded as 138 mm long, under the misidentification of *Lampetra planeri,* by Hubbs (1925: 594).

Associated species reported by Rutter are, for North Fork, *Catostomus occidentalis* Ayres, *Rhinichthys osculus* (Girard) subsp. (as "*Agosia robusta*"), and *Salmo gairdnerii* Richardson (as "*S. irideus*"); and, for South Fork, *Salmo gairdnerii, Rhinichthys osculus* subsp. (as "*Agosia robusta*"), *Gila bicolor* (Girard) subsp. (as "*Rutilus bicolor*"), and *Cottus pitensis* Bailey and Bond (as "*C. gulosus*"). This *Cottus* record has been referred by Bailey and Bond (1963: 20) to their new species, *C. pitensis,* which is endemic in the Pit and Little Sacramento river systems.

2. Head of Fall River, in the west-central part of T 38 N, R 4 E, near the northeastern corner of Shasta County, close to the settlement of Dana and about 5 km north of Fort (Soldier) Mountain; altitude ca. 1020 m. This sizable stream (in the river proper about 50 m wide and uniformly about 0.7 m deep), flowed with a slight to moderate current. It originated in a partly forest-bordered, naturally ponded pocket of springs (Figure 4). Above the spring-fed origin of the river, the stream course (known as Bear Creek, though labelled "Fall River" on some maps) is intermittent; it was dry when examined in the very dry year of 1934. Locally we heard it claimed that the big springs arise from Tule Lake (presumably not the small "Tule Lake" close by to the east) and Lost River (both in the Klamath River system far to the north). However, it seems plausible that the source lies at least in part in the extensive lava beds immediately to the northwest, in southeastern Siskiyou County.

This large cold stream has doubtless been a holdout, during periods of desiccation, of relict species. The stream, within 0.5 km of the springs, yielded, in addition to the lampreys, the endemic sculpin *Cottus macrops* Rutter (1908: 146–147, fig. 4) and *C. asperrimus* (misspelled "*asperrima*") Rutter (1908: 144–145, fig. 3), both closely related to endemic species of the Klamath River system. Rutter's list also included *Salmo gairdnerii,* along with dried remains of *Catostomus occidentalis,* from about a lateral spring, that indicated a prior breeding run of this sucker. The sculpin that Rutter (1908: 146) reported from Fall River as "*C. gulosus*" has been referred by Bailey and Bond to their *C. pitensis.*

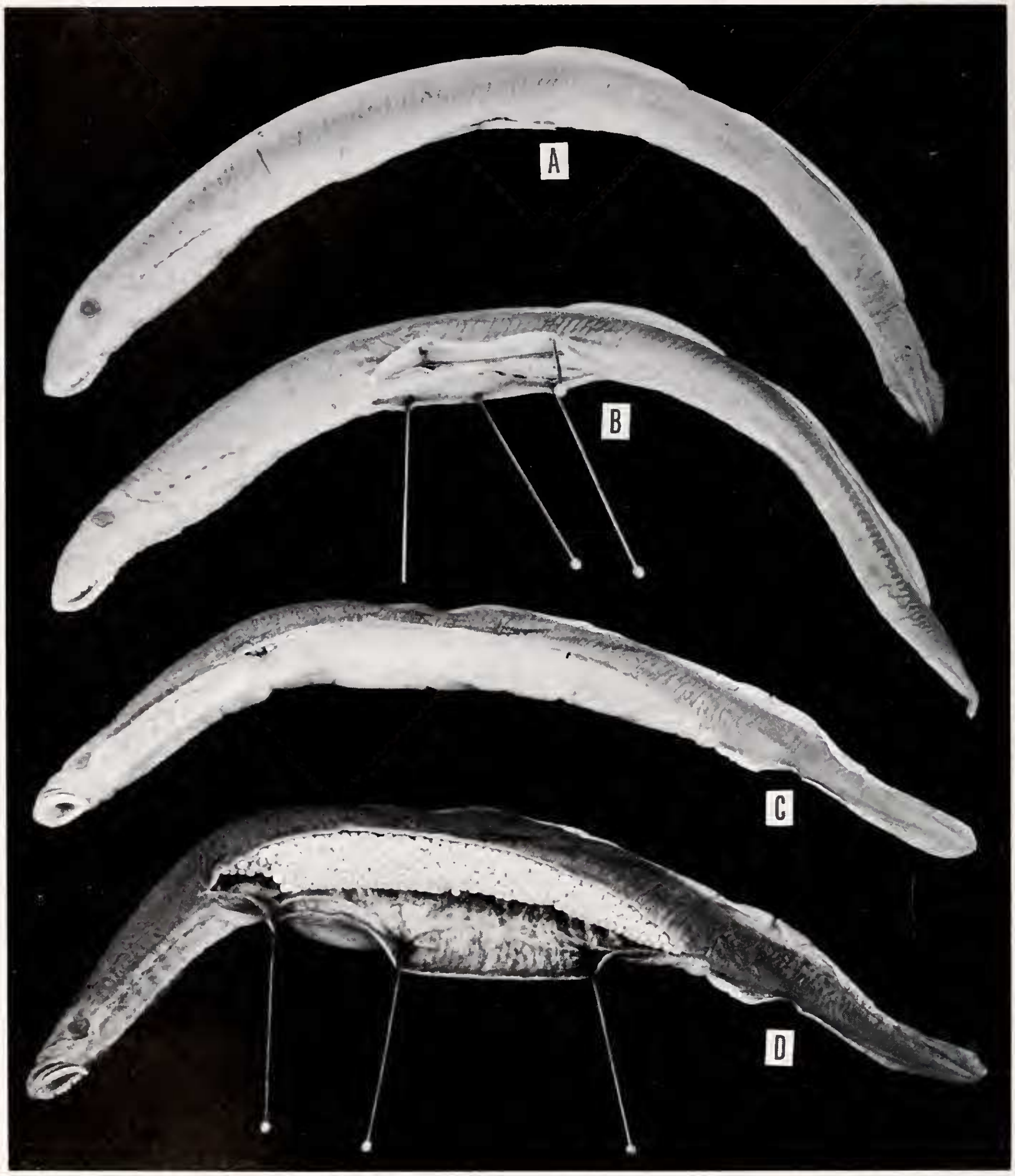

Figure 1. Types of *Lampetra lethophaga*, from head of Fall River, Shasta County, California (Location 2): A, holotype, UMMZ 130648, a mature, neotenic male 128 mm in total length, in side view. B, same specimen, in oblique view, with abdominal wall pinned aside, to show enlarged, lobular testis and atrophic gut bearing signs of hemorrhages. C, paratype, in series UMMZ 130649, a fully mature, neotenic female 116 mm long, in side view. D, same specimen, in oblique view, with abdominal wall pinned aside, to show celome packed full of ripe ova aligned in alate rows.

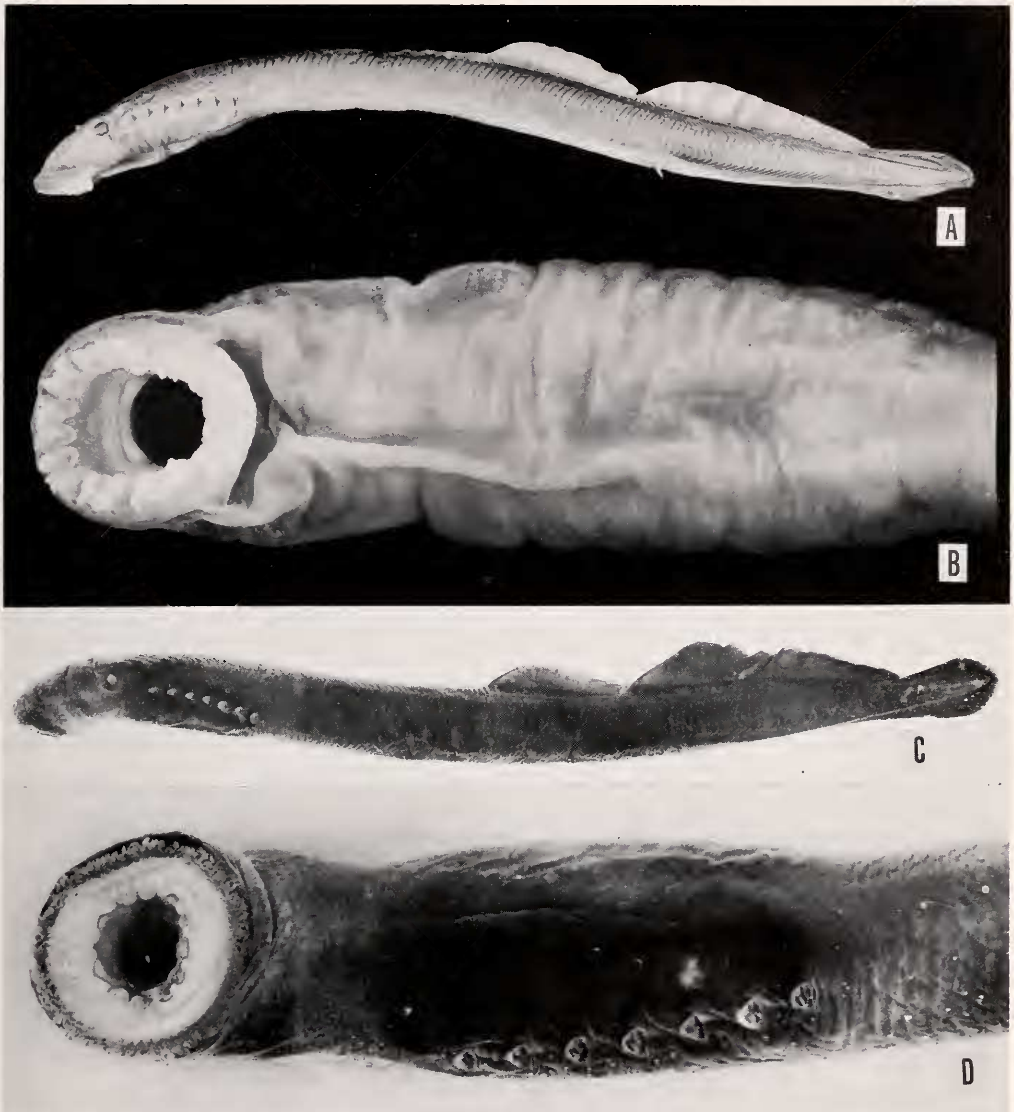

Figure 2. Nuptial males of genus *Lampetra*, subgenus *Entosphenus:* A, *Lampetra lethophaga*, OS 2856 (specimen K0010), 154 mm in total length, in side view; from Crooked Creek, Klamath County, Oregon (Location 11). B, same specimen, in ventral view of head region, enlarged. C, *Lampetra* sp., seemingly intermediate between *L. lethophaga* and precocious forms of *L. tridentata;* SIO 65–144, 176 mm long, in side view; from Willow Creek, tributary to Clear Lake Reservoir, Modoc County, California. D, same specimen, in ventral view of head region, enlarged; with mouth pressed open.

The water was so crystal clear that the bottom seemed to rise ahead. Vegetation comprised patches of *Myriophyllum* and very thick clumps of moss on lava rocks. The bottom in the stream was fine gravel and sand, with scattered lava rocks. The temperature was 11.4° C in the current from a spring and 13.3° C in the river, when the air temperature was 29.4° C. The collection (M34-135) was made by Carl L. Hubbs and family on August 17, 1934, using 4-foot and 6-foot Common Sense woven-meshed seines. One full-grown ammocete and 3 transformed adults came from weeds in the river; one adult was in muddy sand along the bank; the others, all adults, were taken under flat stones lying on clean, coarse gravel in the current from a lateral spring, mostly from under one stone where, when the stone was first turned, they looked like a breeding pod.

The specimens taken at this station are the only ones designated as types. The holotype (UMMZ 130648), 128 mm in total length, is a mature male (Figures 1A–B). The paratypes (UMMZ 130649) comprise one male ammocete 130 mm long, 4 males and 5 females, nearly to quite ripe, 116–142 mm long, and one male that was taken partly decayed, within the same size range. A fully mature female, the smallest specimen, is illustrated (Figures 1C–D).

On the basis of his field work Rutter (1908: 110) described Fall River and the adjacent part of Pit River as follows:

> The upper Pitt River, above the mouth of Fall River, was nearly dry in August, 1898. The water it contained was of a slightly milky color. The rocks at the bottom were covered with a spongy slime . . .
>
> At Fall River Mills, Pitt River receives Fall River, a stream about 100 feet wide and 4 feet deep, with a strong current, but only about 15 miles long. Fall River takes its rise in two or three large springs near Dana, and flows several times as much water as Pitt River above their union. The water is clear and cool and the bottom gravelly, making an excellent spawning stream for salmon, but difficult to attain on account of the steep rapid at its mouth, as well as the fall in Pitt River [see map, Figure 3].
>
> Above the mouth of Fall River for a few miles, Pitt River is broad and deep, but without any perceptible current. Below the mouth of Fall River the character changes entirely. It is broad but shallow, very swift, with many rapids, and makes a rapid descent to the falls [3 km southwest of the mouth of Fall River]. Pitt River Falls, which are 65 feet high, are thought by many to rival in beauty any to be seen in Yosemite Valley. The middle portion is a sheer fall, but each side is broken by ledges, so that it is possible in high water for fish to pass. A fish ladder has been blasted out of the rock near the left bank, and salmon now go over the falls in considerable numbers.

The falls do not delimit the distribution of *Lampetra lethophaga* (nor of the endemic *Cottus pitensis* Bailey and Bond, 1963: 20–25, figs. 1d, 3b, 4d) in the Pit River system, but other Pit River endemics, *Catostomus microps* Rutter (1908: 120–121, fig. D), *Cottus asperrimus*, and *C. macrops* do appear to occur only above these falls.

3. Lower Hat Creek, below Highway 299 bridge, over a stretch of about 6 km, above Lake Britton (an artificially ponded section of Pit River), in northeastern Shasta County; altitude ca. 850 m. On October 4, 1968, lampreys by good fortune were taken and preserved during a massive poisoning by the California Department of Fish and Game, for the removal of "rough" fish, presumably in the hope of controlling predation on and competition with the favored gamefish. Dr. Roger A. Barnhart, Leader of the California Cooperative Fishery Unit at Humboldt State College, who participated in the operation, preserved the fine series of specimens that he has made available for the present study. Dr. Barnhart reported (pers. comm., 1970) that "the lamprey turned out to be quite numerous in this section of Hat Creek. . . . We turned up 2–3 brook lampreys in our fall electrofishing census last fall so apparently we did not obtain a complete kill of lamprey" (again by good fortune).

The collection furnished by Dr. Barnhart comprises 2 ammocetes 91 and 144 mm and 107 transformers 134–199 mm long, of which 12 transformers (SIO 71–8) are retained at Scripps Institution. Nine other specimens (2 ammocetes 56 and 91 mm long and 7 transformers 146–178 mm long; CAS 13391) were collected by Leonard O.

Figure 3. Natural lakes and streams of the entire Pit River drainage basin and the upper part of Klamath River system, showing all known Locations, numbered 1-11, for the nonparasitic *Lampetra lethophaga;* also some waters inhabited by parasitic forms of the same subgenus in the Klamath basin. The collection stations for samples of the precocious stocks of *L. tridentata* utilized in this report are shown at A, for Shasta River near junction with Klamath River; B, for Klamath River at Klamathon; and C, for the Copco Lake impoundment of Klamath River. Shown also are nearby waters of contiguous drainage basins. Two of the largest of the many marshes in the area are Klamath Marsh (KM) and Sycan Marsh (SM).

Map based largely on the United States Geological Survey 1:500,000 state maps of Oregon and California and on the following National Topographic Maps of the 1:250,000 series: Medford, Crescent, Klamath Falls, Weed, Alturas, and Susanville (1955-1963). The natural limits of South Klamath Lake, Tule Lake ("Rhett Lake" on some old maps), and Clear Lake (of the Klamath system) and of the seldom attained outlet stage of Goose Lake are taken chiefly from three old one-degree U.S.G.S. topographic sheets 1:250,000: Klamath, Oregon (1894), and Alturas and Modoc Lava-Bed, California (1892). The Map of the Lake Region of Southeastern Oregon by Snyder (1908a) was also used.

Fisk and W. E. Schafer of the California Department of Fish and Game during the same poisoning.

4. Pit River at Pit 4 Powerhouse, in northeastern Shasta County, 20 km northwest of Burney and 1 km south of Oregon line; altitude ca. 650 m. One transformed female (CAS 25959), 155 mm long, with developing eggs; collected by W. Rowley with electric shocker on June 2, 1953.

5. This number comprises two collections, only approximately located, in the same general area along Pit River, in Shasta County; altitude ca. 550 m:

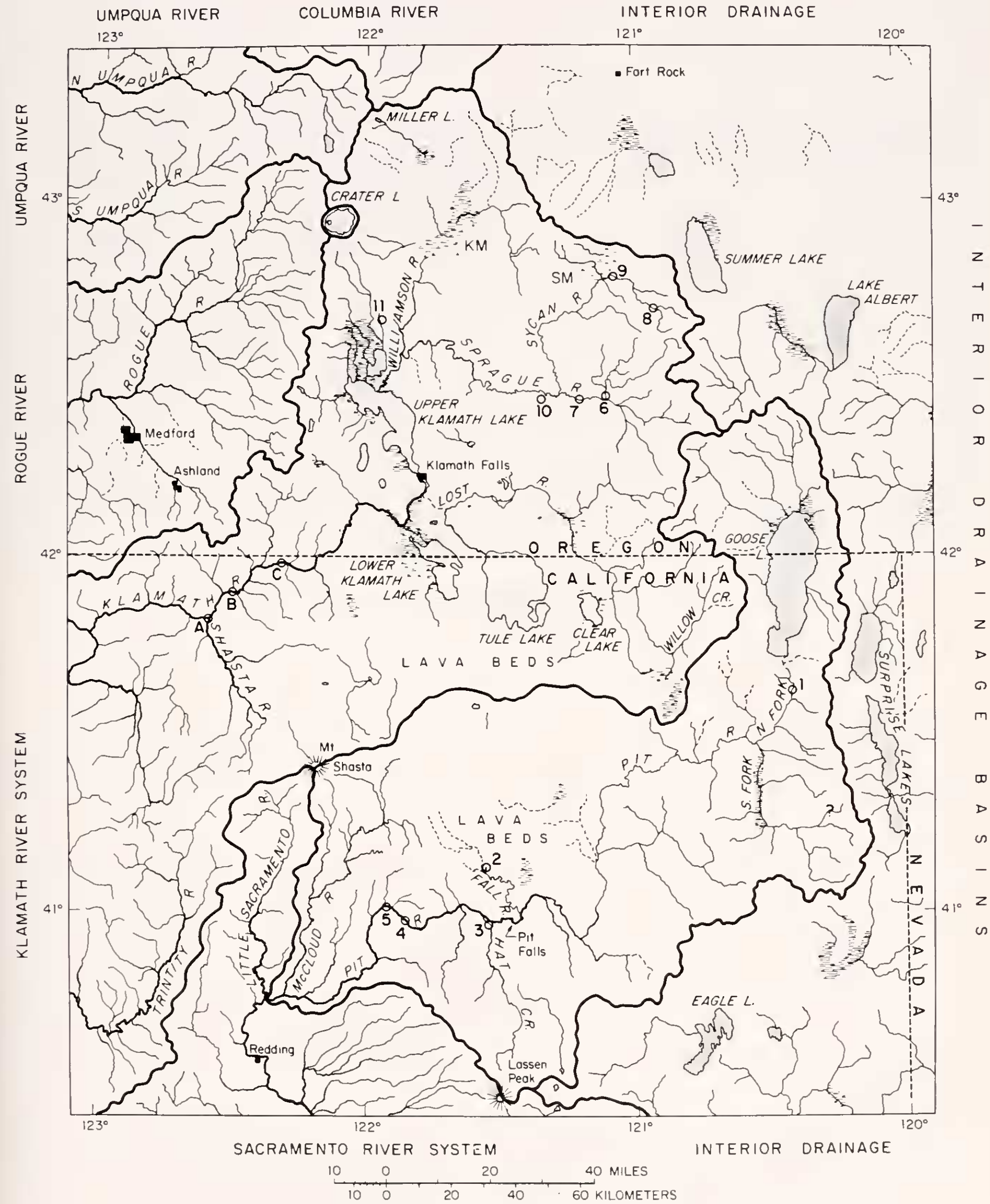

Figure 4. Spring source of Fall River, in naturally ponded pocket of springs immediately above origin of stream flow (the type locality of *Lampetra lethophaga*); Location 2 on distribution map (Figure 3). Photograph by Laura C. Hubbs, August 17, 1934.

5A. Near Big Bend, collected May 3, 1944 (no further data): 7 ammocetes (CAS 13392), 52–124 mm long; ova developing in largest one.

5B. Between Pit 5 Powerhouse and Pit 5 Dam, collected June – September, 1953 by William Rowley, Brian Curtis, and W. O. Cheney, of California Department of Fish and Game, by electric shocker: 1 ammocete (CAS 25968), 63 mm long (identification presumptive).

LOCATIONS IN KLAMATH RIVER SYSTEM, SOUTHERN OREGON

6. North Fork of Sprague River, in east channel, about 1 km above junction with South Fork (prior to extensive disruption of stream course for irrigation), just east of east boundary of Klamath Indian Reservation, near center of west border of T 36 S, R 14 E, eastern Klamath County (Sprague River joins Williamson River just before that stream enters Upper Klamath Lake); altitude ca. 1340 m. Water moderately clear (bottom visibility about 1 m), shaded by 2-m banks, in pasture; some vegetation in patches; temperature cool; current moderate to swift; width ca. 5–8 m; depth ca. 0.7 m. The collection, M34–120b, by Carl L. Hubbs and family, on August 9, 1934, with 25-foot bag seine, contained one adult male (UMMZ 130573) with maturing testis, with tail 43 mm long (front end missing; estimated original total length about 143mm) and one male ammocete, 91 mm long, secured by much stranding of bottom material. Associated fish species were: *Salmo gairdnerii*, *Catostomus snyderi* Gilbert, *Rhinichthys osculus klamathensis* (Evermann and Meek), *Gila caerulea* (Girard), and *Gila b. bicolor*.

7. Sprague River opposite Ferguson Butte (in narrows of a broad valley), 6.5 km inside Klamath Indian Reservation, in T 36 S, R 13 E, Klamath County; altitude ca. 1325 m. Water moderately clear (bottom visibility ca. 1 m); water buttercup and other plants in dense patches; bottom mostly sandy, becoming dirty in weeds, some gravel, mostly fine, few stones; temperature cool; current mostly slight to moderate; width uniformly ca. 12 m;

depth to 1.2 m. The collection, M34–121, by Carl L. Hubbs and family, on August 10, 1934, with a 6-foot woven-mesh seine, contained a recently transformed male 145 mm long (UMMZ 130576), with testis developing and gut reduced, taken in dense vegetation. Associated species were *Salmo gairdnerii*, *Rhinichthys osculus klamathensis*, *Gila caerulea*, *Gila b. bicolor*, and *Cottus klamathensis* Gilbert.

8. Tributary, near mouth, to upper course of Sycan River (affluent to Sprague River), at Pikes Crossing, 3 km south of Currier Camp, near center of T 33 S, R 15 E, eastern Klamath County; just above a major canyon in river course; altitude ca. 1760 m. Water described as white, very slightly turbid, odorless; some green algae; bottom of sand, coarse gravel, and stones; 23.5° C (air 24.5° C); shore a sage flat, with meadow and timber; current swift in part; nearly 7 m wide in places and to 1.5 m deep. The collection, M 39–18, by Robert Rush Miller and Ralph G. Miller, on June 27, 1939, with 9-foot and 15-foot seines, contained an ammocete (UMMZ 136683) 132 mm long, with small testis, and an adult female 106 mm long, somewhat bobtailed, with nearly ripe ova. Associated species, taken both in tributary and river, were *Salmo gairdnerii* and *Rhinichthys osculus klamathensis*.

9. Sycan River where it enters Sycan Marsh, at ZX Ranch, near center of T 32 S, R 14 E, in western Lake County; altitude ca. 1525 m. Water clear, whitish-brown, odorless; without vegetation; bottom of silt, rocks, and brush, largely scoured; 19.5° C (air 13°); willow thickets along shore, margining meadow; current none to slight; width to 5 m in pools; depth to 0.5 m. The collection, M 39–17, by Miller and Miller, on June 26, 1939, with 6-foot and 9-foot seines, contained (UMMZ 136678) an ammocete 121 mm long, with minute gonad, and a female 110 mm long, with large ova. Associated species were *Catostomus snyderi*, *Rhinichthys osculus klamathensis*, and *Gila b. bicolor*.

Dr. Robert Rush Miller was told by personnel at ZX Ranch that the expansive Sycan Marsh (SM, Figure 3) had no open springs and was not known to contain fish. However, it presumably passes fish in high water.

10. This collection, comprising 2 spawning males (Cornell University 10296), 125 and 145 mm long, is labelled "Oregon, 5 mi. W. of Beatty, spring on S. side of road, Apr. 6, 1942, A. H. Wright." This places the station approximately 3–4 km south of midlength of Sprague River, near mid-west border of T 36 S, R 13 E, Klamath County; altitude ca. 1280 m. Dr. Wright stated (in letter of October 1, 1942) that:

> In a swampy area near a small streamlet west of Beatty, Oregon, I happened to find two clear, sandy areas about five or six feet deep. The swampy stretch was so treacherous that someone had laid boards across it and as I looked in the clear areas, . . . among the boiling sand were these two lampreys. It was a very striking spring with a very pronounced boiling sandy bottom.

11. Klamath State Fish Hatchery, in the Klamath Indian Reservation, on Crooked Creek, a short spring-fed stream that joins Wood River close to Agency Lake; in Section 6 of T 34 S, R 7½ E, 4 km northerly from

Table 1. Material of *Lampetra lethophaga* of different stages, arranged chronologically by day of collection

Date of Collection	Locality no.	No. of specimens (and length in mm) at each stage: Ammocetes	Transformers	Maturing and mature adults[1]
Feb. 16 (1961)	11C	—	—	**6(130–160)**
Mar. 13 (1970)	11D	—	—	**6(132–154)**
Mar. 20 (1970)	11E	—	—	**1(137)**
Apr. 6 (1942)	10	—	—	**2(125–145)**
May 3 (1944)	5A	7(52–124)	—	—
May 16 (1970)	11F	6(88–191)	—	—
June 2 (1953)	4	—	—	1(155)
June 26 (1939)	9	1(121)	—	*1(110)*
June 27 (1939)	8	1(132)	—	*1(106+)*
June-Sept. (1953)	5B	1(63)	—	—
Aug. 9 (1934)	6	1(91)	—	1(ca. 143)
Aug. 10 (1934)	7	—	—	1(145)
Aug. 13 (1934)	11A	34(18–155)	—	—
Aug. 17 (1934)	2	1(130)	—	*11(116–142)*
August (1949)	11–	4(70–107)	—	—
Sept. 4 (1898)	1	1(105)	1(142)	—
Oct. 4 (1968)	3	4(56–144)	114(134–199)	—
Oct. 20 (1952)	11B	91(37–205)	—	—

[1]Maturity indicated by boldface type for nuptial and postnuptial stages; by italic type for very definitely maturing stages, including, for the August 17 type series, some fully mature but not in nuptial color and form; and by roman type single specimens in earlier stages.

Klamath Agency, Klamath County; altitude 1280 m. Water very clear, arising in springs on hatchery grounds, close to upper part of Crooked Creek; with thick clumps of submerged vegetation; bottom of sand and pumice stones, with a little muck mixed with sand in the vegetation; shore grassy with some willows, in meadowland; 7.8° C (hatchery personnel reported virtually no fluctuation); current moderate to, mostly, swift; width of rather straight course 4–8 m; depth to 0.6 m.

This ecological description is based on observations on August 13, 1934, when Carl L. Hubbs and family collected 34 ammocetes (UMMZ 130606), 18–155 mm long, with a 6-foot fine-woven-mesh seine, by vigorously working through thick weed beds, muddy-sand bars, etc. None of the specimens showed any sign of metamorphosis, which may well take place late in this very cold water. The hatchery superintendent (W. I. Howland) provided evidence that "runs of eels" do not occur in this or other local streams, and gave information on the local occurrences of lampreys. Some of the larger ammocetes show some development of ova and of testis. It was therefore concluded, on this initial contact, that the local lampreys are nonparasitic dwarfs.

Associated with the ammocetes in the 1934 collection (M 34–126), in addition to *Salmo gairdnerii* and *Salvelinus fontinalis* (Mitchill) were sculpins, of the Klamath cold-water endemic species *Cottus tenuis* (Evermann and Meek), which was common. The superintendent had 3 or 4 large adults of *Catostomus snyderi*, which he said runs up Wood River and Crooked Creek in early spring. He indicated that still larger suckers, which from his description seemed to be *Chasmistes*, run chiefly up Williamson River, early in the spring, to spawn, and some go up Wood River. Eggs of these large suckers, he said, cover the bottom near wiers across Williamson River to a depth of several inches. When they come, the trout run ceases.

Dr. Carl E. Bond (pers. comm., 1970) has received similar testimony regarding the local lampreys from personnel of the Klamath Hatchery. He has kindly provided me with additional specimens (listed in Table 2 as from Locations 11B–F), taken by and for them at the hatchery, in the ponds and their discharges ("after passing through the ponds, water is channeled into two ditches that run a short distance to Crooked Creek."). The 13 adults examined in these lots, from Locations 11C–E, are all in nuptial or postnuptial color and form (one, a partly spent male 154 mm long, the largest in 11D, is illustrated as Figure 2A–B). Habitat data for the collection of March 20, 1970 (CEB 70–2; listed in Table 2 as from Location 11E), by Dr. Bond, Mr. Kan, and Richard Wilmot, by "sculpin net (frame net)" are: water clear, with *Ranunculus*, mostly at edges and behind stones; bottom of sand and fine gravel, with few large stones; temperature 6.7° C; shore of masonry or stone; current moderate to slow; width 2.5–5 m; depth to 0.6 m. Lampreys taken in this collection were 2 ammocetes and 4 adults (1 alive and 3 dead), but the one adult received for study is a ripe male 137 mm long.

ZOOGEOGRAPHICAL CONSIDERATIONS

Like most but not all of the nonparasitic forms of lampreys, *L. lethophaga* lives within the range of its assumed parental type (see discussion of Life History, and Hubbs and Potter, in press). So far as known, it is limited to the upper parts of the Pit River system of the Sacramento River drainage in northeastern California and of the Klamath River system, adjoining, in south-central Oregon (Figure 3). This form, and/or parallel-derived nonparasitic types, may yet be discovered elsewhere within the wide range (Figure 5) of *L. tridentata*, but the only nonparasitic lampreys previously known to occur around the North Pacific are the derivatives of *Lampetra (Lampetra) ayresii* (Günther) in the northeastern Pacific drainages (Vladykov and Follett, 1958, 1965), occurring as far south as the Santa

Table 2. Material of *Lampetra lethophaga* from Klamath State Fish Hatchery received from Carl E. Bond and Ting T. Kan

Locality	Date collected	Coll. no. (OS)	Collector	Number (total length, mm): Ammocetes	Number (total length, mm): Nuptial & postnuptial
11B	Oct. 20, 1952	2860	Kenneth Cochrun	25(77–189)[1]	——
11C	Feb. 16, 1961	2855	Do.	——	6(130–160)
11D	March 13, 1970	2856	Ore. Game Comm.	——	6(132–154)
11E	March 20, 1970	2858	Bond, Kan, Wilmot	——	1(137)[2]
11F	May 16, 1970	2859	Bond, Johnson, Kan	6(88–191)	——

[1]Kan measured 66 additional ammocetes, as 37–205 mm in total length, from this collection, which was supposedly taken by electrofishing, and 4, of 70–107 mm, collected at the same hatchery in August, 1949. These measurements have been included in the size-frequency graph (Figure 8).

[2]Collection sheet lists for this set 2 ammocetes and 4 adults (1 alive and 3 dead).

Ana system of streams in southern California, and the derivatives of *Lampetra (Lethenteron) japonica* (Von Martens), ranging from northern China and southern Japan through the coastal regions of Siberia to Alaska (and in northeastern North America). Sufficient material is known to render it highly probable that any other regional occurrences of any nonparasitic derivative of *Lampetra (Entosphenus) tridentata* are at most few and limited.

The known distribution of the nonparasitic lampreys around the North Pacific appears to be complementary. The ranges of the widespread nonparasitic representatives of the subgenera *Lethenteron* and *Lampetra* apparently do not overlap, and although *L. lethophaga* of the subgenus *Entosphenus* occurs about midway in the range of the Pacific-drainage representatives of subgenus *Lampetra*, no trace of that subgenus has been found in the Pit or Klamath systems, either by me, or by Carl E. Bond (pers. comm., 1971).

It is noteworthy that no nonparasitic forms of the *Entosphenus* complex have been discovered in other parts of the long range of *Lampetra tridentata* around the periphery of the North Pacific (Figure 5), which extends southward from Bering Sea and Unalaska (Jordan and Gilbert, 1899: 434; McPhail and Lindsey, 1970: 58), and from Bering Island (Svetovidova, 1948; Berg, 1948, Addenda; 1962: 494). The limits of the known distribution of the parasitic form (or forms) have been expanded southward on both sides of the Pacific. On the American side it has been taken in streams as far south as southern California and in the ocean off Baja California, Mexico (Hubbs, 1967). On the Asiatic side there are several records from Japan, stated below. There seems to be no valid report of *L. tridentata* from the mainland of Asia (Lindberg and Legeza, 1959: 17–18 and 1967: 20–21), where *L. japonica* holds forth (the record of "*Entosphenus tridentatus*" from Kamchatka by Jordan and Evermann, 1900: 3231, pl. 1, fig. 4, was apparently based on the ammocete that was listed by Jordan and Gilbert, 1899: 434, from a river near Petropaulski, Kamchatka, as "*Entosphenus camtschaticus*," though on circumstantial grounds it seems more probable that it was an example of *L. japonica*). Okada and Ikeda (1938: 140–141)

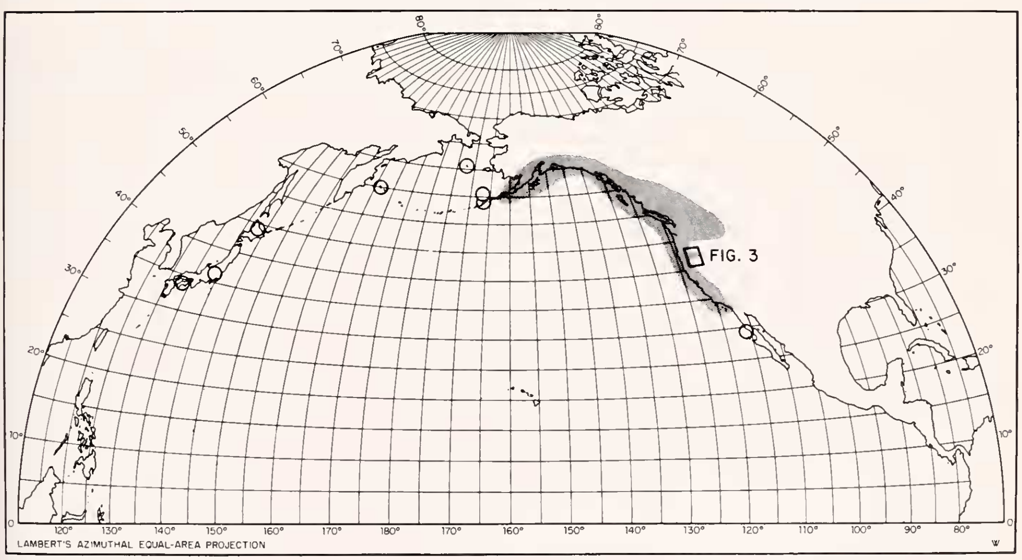

Figure 5. Distribution of *Lampetra tridentata* around margin of North Pacific Ocean. Assumed usual range stippled; record stations beyond these limits ringed; area shown in Figure 3 indicated.

initiated the Japanese records of *L. tridentata* by listing a specimen from Yahutugawa (river) in the Okhotsk Sea drainage of Hokkaido. Nemoto (1955: 69–70) stated the range of the species as "the broad region from the Arctic as far south as southern California and down to about 35° N Latitude in the western side of the Northern Pacific," but gave no supporting documentation for either the Arctic or for the southwestern limit, other than the questionable basis of finding, in the western North Pacific, whales bearing scars showing the tooth marks of *L. tridentata.* Aoyagi (1957), however, reported the capture of a specimen of this species in central Honshu, near 36° N latitude, in Kinugawa (river) at Atsutamura in Tochigi-ken. A further extension of range of the species has now come to light: Dr. O. Okamura has obtained a specimen from Yoshinogawa (river) on Shikoku Island in southern Japan; Tamotsu Iwai (pers. comm., 1970) has verified the identification.

The occurrence of the nonparasitic representative of the *Entosphenus* group in the adjacent basins of the Pit and Klamath rivers is not unique, for these stream systems harbor a number of other endemic fishes, some of which are sympatric with *Lampetra lethophaga.* Klamath endemics were described by Gilbert (1898) and by Evermann and Meek (1898). One of these species, *Catostomus rimiculus* Gilbert (1898: 3) was described from the Klamath River system only but it was later found (Snyder, 1908b: 161) to inhabit also the Rogue River system, which adjoins the Klamath River drainage basin (Figure 3); it may well have crossed over the divide by some fluvial connection. The peculiarities and endemism of the Klamath and Pit river systems were summarized by Hubbs and Miller (1948: 67–71). *Catostomus microps* is a Pit endemic (Rutter, 1908: 120–121) and *Cottus pitensis* Bailey and Bond (1963: 20–24) is known only from drainages of the Pit River and the contiguous Little Sacramento River. An additional indication of residual endemism in the fish fauna of the area under consideration appears to be coming to light: Behnke (1970: 241) has referred to "a group of previously undescribed trout native to several desiccating basins in southern Oregon extending to the Pit and McCloud rivers of northern California."

DESCRIPTION AND COMPARISONS

The specifications, here adopted, of meristic and morphometric characters, involving definitions and methods, are essentially those proposed by Hubbs and Trautman (1937: 27–43, figs. 1–5). They have been adopted also by Hubbs and Potter (in press) in their account of the distribution, phylogeny, and taxonomy of lampreys.

Chief concern pertains to the designation and to the method of counting of the lingual, oral, and disc teeth, which have been illustrated for *Lampetra (Entosphenus) tridentata* by Hubbs (1947, fig. 3; 1963, fig. 2), by Vladykov and Follett (1958, fig. 1; 1965, fig. 1; 1967, fig. 2), and by Hubbs and Potter (in press, fig. 7). Special points regarding the cusps on the lingual laminae (one transverse and two longitudinal) and on the oral laminae (the supraoral and the infraorbital) are discussed below, in the description of the dentition.

The concept of the circumoral row or series of teeth proposed by Hubbs and Trautman, primarily on the basis of the generalized dentition of *Ichthyomyzon,* seems quite applicable to the *Entosphenus* group, particularly because the posterior circumorals are so definitely aligned with the lateral circumorals, just outside the infraoral lamina. Furthermore, the lateral and posterior circumorals intergrade, through the frequent and unique bicuspid structure, and often through the increasing dilation outward, of one or more of the most lateral and most anterior of the posterior circumorals. Although the alignment of the posterior and lateral elements in a circumoral row is clear, the alignment and method of counting of the anterior connective is complicated by the tendency of all the anterior teeth in this group to alternate (in quincunx), so that a rather arbitrary distinction is involved, as is described below. The alignment and nomenclature of the inner disc teeth championed by Vladykov and Follett contrasts with the system of Hubbs and Trautman, in that the anterior circumorals are treated as the inner "anterials," the lateral circumorals as the "inner laterals" or "endolaterals," and the posterior circumorals as the inner "posterials."

Because dentition has traditionally and rightfully been emphasized in the systematics of lampreys, with added stress by Hubbs and Trautman (1937), by Vladykov and Follett (1967), and by Hubbs and Potter (in press), the dental laminae and teeth are here treated first.

DENTITION

Distinctive features of the dentition of *Lampetra lethophaga* outlined in the Diagnosis seem to make clear the relationships as well as the distinctness of this nonparasitic representative of *L. tridentata*. Exhibited are some features of reduction and some of increased variability. Reduction (often a concomitant of dwarfism) is indicated by the frequent degeneration, or loss (Table 3), of the median cusp of the supraoral (the tricuspid supraoral has usually been emphasized — often overemphasized — as the main feature of the genus or subgenus *Entosphenus*); by the occasional reduction of infraoral cusps to 4; by the frequent reduction (Table 4) by 1 cusp on any of the four lateral circumorals, from the normal *Entosphenus* formula of 2–3–3–2 (Figure 7); and by the low number (9–15) of posterior circumorals. The number of cusps in the transverse lingual lamina also seems to be reduced. Furthermore, the teeth tend to be reduced in size; the lingual and oral laminae and, in particular, the lateral circumorals, are all less dilated than in typical *L. tridentata*, and the other teeth tend to be smaller and less robust. Increased variability (commonly associated with degeneration) is shown strikingly by the number of cusps on the supraoral and, less certainly, by the number of infraoral cusps (Table 3), and, definitely, by the number of cusps on the lateral circumorals (Table 4).

The small size of *L. lethophaga* and the weakness of its dentition render cusp counts at times somewhat difficult. Adequate magnification with strong illumination supplemented by a fine jet of compressed air may be called for.

Although the full development of the teeth is a relatively transient feature, the cusps at early stages are sharp. In fact, it is difficult to determine from the teeth, at prime development, whether a specimen represents a parasitic or a nonparasitic form. The lingual laminae atrophy first, in concordance with the elimination of feeding. Of the disc teeth, the outer ones, between the circumorals and the marginals, appear to be the first lost. The degeneration of the anterior circumorals seems to follow soon; they become unrecognizable while the posterior circumorals remain sufficiently developed to be seen. The lateral circumorals are among the last to disappear, or to fragment. Completely spent individuals retain very little of their dentition, and the teeth do not seem to fuse into a cornified mass, as they do in *L. tridentata*.

Lingual laminae.— In correlation with the reduced size of the laminae, the cusps are small — often minute, weak, and crowded. The median tooth of the transverse lamina is usually only weakly to moderately enlarged, and is somewhat variable: it is occasionally partly fused with an adjoining cusp on either side, and is rarely doubled. The transverse lamina is nearly rectilinear, with only the outer ends curved backward. The number of cusps in this lamina is probably reduced, totally only 12–19 in the 11 countable laminae, with a mean of 15.6 (12–17, averaging 14.75 in 8 from Pit River, 19 in two from the Sycan River, and 16 in one from Crooked Creek). The counts for the 15 specimens from the Klamath River near Klamathon are higher, 21–27 (mean 23.3), and the one from Copco Lake has 22. However, the counts for 437 macrophthalmiae of *L. tridentata* from the mouth of Shasta River, not far distant, are intermediate: 14–23 (mean 18.1). McPhail and Lindsey (1970: 57) described the lamina of *L. tridentata* as having "about 15–25 fine points, the median one scarcely larger than the others."

The cusps on the longitudinal lamina are also minute and relatively very numerous. They were not counted. McPhail and Lindsey (1970: 53) stated that "*E. tridentatus* has 50–63 fine points on each longitudinal lingual tooth plate, in contrast to 0–26 points in all *Lampetra* species examined," and they regarded this distinction as one basis for the recognition of *Entosphenus* as a distinct genus. The number of cusps no doubt varies, and the "O" counts presumably represent laminae that have been shed, probably postnuptially. The other basis given for the recognition of *Entosphenus* was the number and arrangement of the velar tentacles — a feature (not checked by me) that hardly seems of generic significance, though seemingly trenchant on the species level.

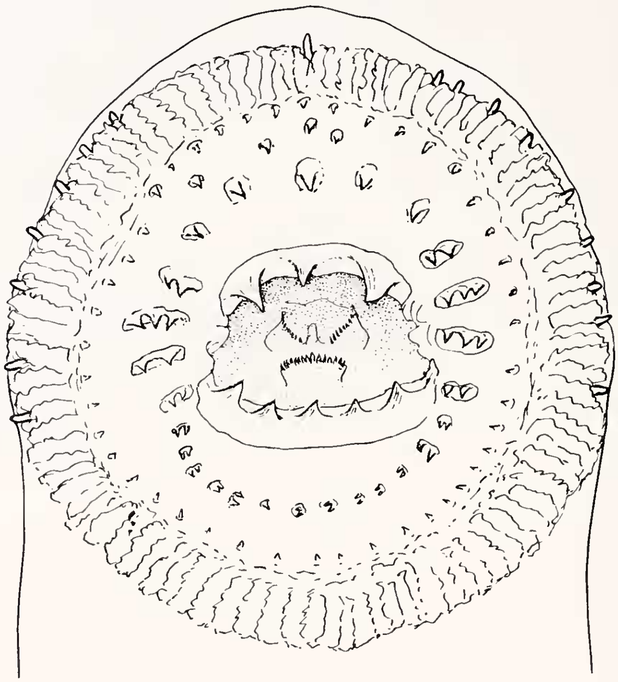

Figure 6. Dentition of *Lampetra lethophaga*, from mature female paratype 116 mm long, shown in Figures 1 C, D; note oral papillae as well as fimbriae; development of bicuspid posterior circumorals is extreme in this specimen.

Oral plates (Table 3).— The oral plates are somewhat more delicate and less dilated than in the parasitic forms of *Entosphenus*.

As noted above, the supraoral plate (or tooth) often fails to exhibit the strongly tricuspid form traditionally used to diagnose *Lampetra tridentata*, for, in each river system, the median tooth is more or less reduced in size, down to a mere rudiment, or is altogether missing. Bicuspids and tricuspids are about equal in frequency, and quadricuspids are occasional. Thus, the supraoral-cusp pattern is much more variable than is usual in *Entosphenus*. Ordinarily, in *L. tridentata*, the tooth is tricuspid, as it is in every one of the 437 macrophthalmiae counted from the mouth of Shasta River, in all 15 adults from the Klamath River, in the one from Copco Lake, and (Mr. Ting T. Kan, pers. comm., 1971) in all 86 adult specimens of the dwarf race from Miller Lake. In *L. lethophaga*, as a further indication of variability, the third cusp is occasionally well to one side of the midline, and the 3 quadricuspid plates exhibit different cusp patterns: 2+2, 1+1+2, and 2+1+1 (left-to-right).

Bond (1961: 14) distinguished the nonparasitic form (his "*Lampetra* sp.") from *L. tridentata* too sharply, as having "teeth dull, supraoral lamina with two widely separated cusps" rather than having "all teeth sharp and functional, supraoral lamina with 3 cusps." This seems to be the commoner condition only in Crooked Creek (Table 3) from which Dr. Bond had specimens of the new form.

The cusps on the infraoral plate average nearly as numerous in *L. lethophaga* as in the precocious stocks of *L. tridentata* from the Klamath River system. Six among 56 specimens have only 4 cusps, whereas reduction below 5 was not encountered among the 453

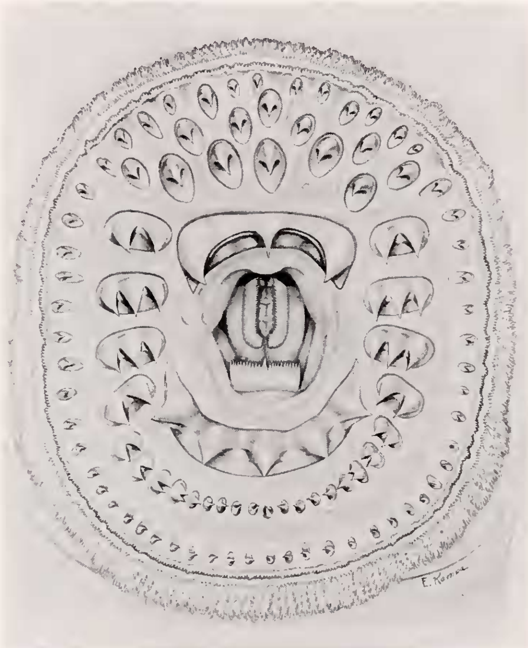

Figure 7. Generalized illustration of dentition of *Lampetra tridentata*, drawn, with mouth somewhat puckered, by Elizabeth M. Kampa; used as basis for figures in Encylopaedia Britannica (Hubbs, 1947, fig. 3; 1963, fig. 2).

specimens of *L. tridentata* listed in Table 3, nor in any of the counts for the Trinity and Eel rivers in northern California. The cusp count was increased in *L. lethophaga* to 6 or 7 in only 7% of the specimens, but in the *L. tridentata* specimens here tallied, to 12% in those from Shasta River and to 33% in those from Klamathon; and the one from Copco Lake has 6 infraoral cusps. Counts higher than 5 may result either from a regularly spaced series or from the interpolation of a small supernumerary cusp toward one end of the plate. The outermost cusp of each side is strengthened but is never doubled, as it typically is in subgenus *Lampetra*. The specimen of doubtful identification from Willow Creek and (Ting T. Kan, pers. comm., 1971) the Miller Lake lampreys have the usual cusp pattern for the oral teeth (3 and 5, respectively).

Circumoral teeth and cusps (Tables 4–6). — Some of the sharpest distinctions of *L. lethophaga* involve these teeth and their cusps, on the lateral and posterior fields of the disc.

Anterior circumorals.— As in *L. tridentata,* the anterior circumorals are typically countable as 5, on the criterion that any anterior tooth is interpreted as a circumoral that approximately reaches or passes behind the imaginary arcuate line passing through the centers of the teeth of the definitely inner-marginal row. The tendency of the anterior oral teeth to alternate so as to approach a quincunx arrangement renders the inclusion or exclusion of a given tooth from the anterior-circumoral series somewhat difficult and rather arbitrary. Another uncertainty is introduced by the tendency for the anterior disc teeth to atrophy rapidly in this species. The counts recorded are 5 for 14 specimens,

Table 3. Counts of cusps on oral plates in *Lampetra lethophaga* and in Klamath River precocious populations of *L. tridentata*

Oral plate / Species / River system (No.)[1] / Locality (No.)[1]	Number of cusps per oral lamina: 1	2	3	4	5	6	7	Mean
Supraoral								
L. lethophaga								
Pit (10)	—	3	5	2[2]	—	—	—	2.90
Sprague (5)	—	2	3	—	—	—	—	2.60
Crooked (13)	—	8	4	1	—	—	—	2.46
Total (28)	—	13	12	3	—	—	—	2.64
L. sp.								
Willow (1)	—	—	1	—	—	—	—	3.0?
L. tridentata								
Klamath (453)								
Shasta R. (437)	—	—	437	—	—	—	—	3.000
Klamathon (15)	—	—	15	—	—	—	—	3.00
Copco L. (1)	—	—	1	—	—	—	—	3.0?
Infraoral								
L. lethophaga								
Pit (10)	—	—	—	1	9[2]	—	—	4.90
Sprague (5)	—	—	—	1	2	1	1	5.40
Crooked (13)	—	—	—	1	10	1	1	5.15
Total (28)	—	—	—	3	21	2	2	5.11
L. sp.								
Willow (1)	—	—	—	—	1	—	—	5.0?
L. tridentata								
Klamath (453)								
Shasta R. (437)	—	—	—	—	382	41	14	5.158
Klamathon (15)	—	—	—	—	10	5	—	5.33
Copco L. (1)	—	—	—	—	—	1	—	6.0?

[1]Number of specimens.
[2]Value for holotype.

doubtfully 5 for 7, 6 for 3, and 7 for 2. The anterior circumorals are counted as 5 also in the Willow Creek specimen of doubtful identification.

Lateral circumorals (Table 4).— A striking feature of *L. lethophaga,* already alluded to, is the strong tendency for the number of cusps to decrease by 1 in each of the consistently 4 lateral circumorals, on each side, from the standard, usually almost invariable, formula of 2–3–3–2 in *L. tridentata.* The ratio of reduced counts to the full

Table 4. Counts of cusps on each lateral circumoral tooth, on each side, in *Lampetra lethophaga* from different river systems and in Klamath River precocious populations of *L. tridentata*

Species River system (No.)[1] Locality (No.)[1]	Tooth no.[2]	Cusps per tooth 1	2	3	4	Mean	Tooth no.[2]	Cusps per tooth 1	2	3	4	Mean
L. lethophaga												
Pit (20)		—	18[3]	2	—	2.10		—	9	11[3]	—	2.55
Sprague (10)		4	5	1	—	1.70		—	5	4	1	2.60
Crooked (22)		4	18	—	—	1.82		—	18	4	—	2.18
Total (52)	(1)	8	41	3	—	1.90	(2)	—	32	19	1	2.40
L. sp.												
Willow (2)		—	2	—	—	2.0?		—	—	2	—	3.0?
L. tridentata												
Klamath (905–906)												
Shasta R. (874)		—	874	—	—	2.000		—	—	873	1	3.001
Klamathon (29–30)		—	27	3	—	2.10		—	—	25	4	3.14
Copco L. (2)		—	2	—	—	2.0?		—	—	2	—	3.0?
L. lethophaga												
Pit (20)		—	19[3]	1	—	2.05		—	20[3]	—	—	2.00
Sprague (10)		—	6	4	—	2.40		2	7	1	—	1.90
Crooked (22)		—	20	2	—	2.09		8	14	—	—	1.64
Total (52)	(3)	—	44	8	—	2.15	(4)	10	41	1	—	1.83
L. sp.												
Willow (2)		—	—	2	—	3.0?		—	2	—	—	2.0?
L. tridentata												
Klamath (905–906)												
Shasta R. (874)		—	—	872	2	3.002		—	855	19	—	2.022
Klamathon (29–30)		—	1	21	7	3.21		—	21	7	2	2.37
Copco L. (2)		—	—	2	—	3.0?		—	2	—	—	2.0?

[1]Number of sides counted.

[2]The teeth are numbered from the anteriormost on each side.

[3]Value for holotype.

complement, for each of the teeth, counted from the front on each side, for each of the three stream systems, is as follows:

First tooth — 0:20 (Pit), 4:10 (Sprague), 4:22 (Crooked).
Second tooth — 9:20 (Pit), 5:10 (Sprague), 18:22 (Crooked).
Third tooth — 18:20 (Pit), 6:10 (Sprague), 20:22 (Crooked).
Fourth tooth — 0:20 (Pit), 2:10 (Sprague), 8:22 (Crooked).

The Willow Creek specimen agrees with *L. tridentata* in the formula of 2–3–3–2. The same formula, with little variation, holds for the dwarfed, reportedly parasitic Miller Lake lamprey (Carl E. Bond and Ting T. Kan, pers. comm., 1971).

Posterior circumorals (Tables 5, 6).— One of the dentitional features that most clearly points to the derivation of *L. lethophaga* from *L. tridentata* is the frequent bicuspid structure of the more lateral of its posterior circumorals (Figures 6, 7), involving teeth occasionally as far from the end as the seventh (Table 5). *Lampetra tridentata* is the only previously known lamprey of the *Lampetra* type that has such bicuspid teeth in the posterior commissure, and this tendency is notably characteristic of the precocious Klamath River types that may well have been ancestral to *L. lethophaga.* In fact, in those types the

Table 5. Counts of cusps on individual posterior circumoral teeth in *Lampetra lethophaga* and in the Klamath River precocious populations of *L. tridentata*

Species / River system (No.)[1] / Locality (No.)[1]	Tooth No. 1[2] U/B—Mean[3]	Tooth No. 2[2] U/B—Mean[3]	Tooth No. 3[2] U/B—Mean[3]	Tooth No. 4[2] U/B—Mean[3]
L. lethophaga				
Pit (20)[4]	8/12—1.60	7/13—1.65	14/6—1.30	18/2—1.10
Sprague (10)	8/2—1.20	8/2—1.20	8/2—1.20	8/2—1.20
Crooked (18)	17/1—1.06	18/0—1.00	18/0—1.00	18/0—1.00
Total (48)	33/15—1.31	33/15—1.31	40/8—1.17	44/4—1.08
L. sp.				
Willow (2)	0/2—2.0?	1/1—1.5?	2/0—1.0?	2/0—1.0?
L. tridentata				
Klamath (906)				
Shasta R. (874)	213/661—1.756	549/325—1.372	835/39—1.045	835/39—1.045
Klamathon (30)	1/29—1.97	1/29—1.97	5/25—1.83	14/16—1.53
Copco L. (2)	0/2—2.0?	0/2—2.0?	0/2—2.0?	0/2—2.0?

Species / River system (No.)[1] / Locality (No.)[1]	Tooth No. 5[2] U/B—Mean[3]	Tooth No. 6[2] U/B—Mean[3]	Tooth No. 7[2] U/B—Mean[3]	Tooth No. 8[2] U/B—Mean[3]
L. lethophaga				
Pit (20)[4]	18/2—1.10	19/1—1.05	19/1—1.05	20/0—1.00
Sprague (10)	10/0—1.00	10/0—1.00	10/0—1.00	10/0—1.00
Crooked (18)	18/0—1.00	18/0—1.00	18/0—1.00	18/0—1.00
Total (48)	46/2—1.04	47/1—1.02	47/1—1.02	48/0—1.00
L. sp.				
Willow (2)	2/0—1.0?	2/0—1.0?	2/0—1.0?	2/0—1.0?
L. tridentata				
Klamath (906)				
Shasta R. (874)	872/2—1.002	873/1—1.001	874/0—1.000	874/0—1.000
Klamathon (30)	25/5—1.17	26/4—1.13	28/2—1.07	29/1—1.03
Copco L. (2)	0/2—2.0?	0/2—2.0?	1/1—1.5?	0/2—2.0?

[1]Number of sides counted (2 per specimen).

[2]The teeth are numbered from the lateralmost and foremost; the ninth tooth is bicuspid on one side of the one specimen from Copco Lake.

[3]U/B indicates the number of unicuspids and bicuspids, respectively, for each given tooth number. The numbers (and the means) are in a sense hypothetical, for it is assumed for all teeth more centrad than the fourth on either side that the tooth, unless bicuspid, would have been unicuspid had such a tooth been present: the total number of posterior circumorals may be as low as 9 in *L. lethophaga* and as low as 15 in the Klamath River precocious populations of *L. tridentata;* hence the tooth count on either side often passes beyond the midline into the series from the other side; the tooth number used assumes the arrangement of unicuspids and bicuspids that would have existed, had there been as many as 9 teeth on each side.

[4]The holotype has the outermost 2 teeth on each side bicuspid.

lateral teeth often grade, in position, size, and structure, almost imperceptibly into the outer members of the posterior series. The proportion of the outer posterior teeth that are bicuspid is greater in the Pit River sample than in the collections from Sprague River and Crooked Creek. Oddly, the degree of bicuspidity averages very distinctly higher in the dwarf adults of *L. tridentata* from the Klamath River near Klamathon than in the macrophthalmiae from the Shasta River near its junction with the Klamath, not far below Klamathon; and the one specimen from Copco Lake has 8 bicuspids on each side (a record number). In compensation, the unilateral posterior circumorals average fewer in the Klamathon lot than in the Shasta River specimens, and the one from Copco Lake has only 3. One of the sharpest distinctions of *L. lethophaga* from the samples of *L. tridentata* from the Klamath River system lies in the lower total number of posterior circumorals, with very little overlap (Table 6). The alignment of the posterior circumorals tends to be slightly irregular in some specimens, though at the end on each side the series lines up very well with the posteriormost (fourth) lateral circumoral.

In the numbers of circumoral teeth and cusps the one specimen of doubtful identification from Willow Creek shows some correspondence with *L. tridentata* and some features of seeming intermediacy between the two species. The total number of posterior teeth in the series (17) is 2 higher than any count for *L. lethophaga* and below the mean for the *L. tridentata* series. The number of unicuspid posteriors (14) is extreme for *L. lethophaga* and near the mean for *L. tridentata*. The number of bicuspid posteriors (total 3) is not definitive.

Outer disc and marginal teeth.— As in *L. tridentata*, the disc is consistently toothless between the circumorals and the marginals, except for a few rather scattered teeth (not counted) in the anterior field. The pattern of the marginal teeth, as in *L. tridentata*, in some specimens, weakly suggests that the marginal series may retain elements from the very tips of the recurved ends of the original alate rows — particularly in that some of the teeth tend to be rather larger and less completely at the disc edge than those preceding and following (see figures by Vladykov and Follett and by Hubbs and Potter and the discussion by the latter authors). The marginal series, however, remains essentially complete and intact, whatever its origin may have been.

In the Copco Lake specimen the marginals between the first and second and between the second and third lateral circumorals are much dilated, and are considerably interpolated between the laterals.

ORAL PAPILLAE

The oral papillae (Figure 6, Table 7), of presumed sensory function, were counted because it was thought that they might be reduced in number in the relatively very small disc of *L. lethophaga*. These structures, which occur around the periphery of the disc among lampreys in general, are almost always distinguishable from the finbriae. They stem from the groove just ringing the slight pad from which the radially transverse fimbriae arise. They are conical and pointed, rather than being truncate with fimbriate edge. They are often irregularly spaced along each side, with a wide intervening separation posteriorly and with a narrow gap anteriorly, normally broken by a more or less precisely median-anterior papilla (rarely missing, doubled, or trebled). Slight uncertainty in counts arises from the rather rare apparent or real intergradation between papillae and fimbriae, at least in superficial aspect. In one specimen from Klamathon, irregularities, involving adventitious creases and folds around the outer part of the disc, render the count useless. A fine jet of air aids in the count.

In mean numbers and in the range of variation, the papillae are rather similar in *L. lethophaga* and *L. tridentata* (also in the specimen from Willow Creek of doubtful

Table 6. Counts of posterior circumoral teeth in *Lampetra lethophaga* and in Klamath River precocious populations of *L. tridentata*

Species River system (No.)[1] Locality (No.)[1]	Total number of posterior circumorals													
	9	10	11	12	13	14	15	16	17	18	19	20	21	Mean
L. lethophaga														
Pit (10)	—	1	1[2]	3	2	2	1	—	—	—	—	—	—	12.60
Sprague (5)	—	1	—	2	1	—	1	—	—	—	—	—	—	12.40
Crooked (8)	1	1	2	2	2	—	—	—	—	—	—	—	—	11.38
Total (23)	1	3	3	7	5	2	2	—	—	—	—	—	—	12.13
L. sp.														
Willow (1)	—	—	—	—	—	—	—	—	1	—	—	—	—	17.0?
L. tridentata														
Klamath (453)														
Shasta R. (437)	—	—	—	—	—	—	1	9	99	209	92	24	3	18.066
Klamathon (15)	—	—	—	—	—	—	—	1	3	6	5	—	—	18.00
Copco L. (1)	—	—	—	—	—	—	—	—	—	—	1	—	—	19.0?

Species River system (No.)[1] Locality (No.)[1]	Total number of bicuspid posterior circumorals																	
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Mean
L. lethophaga																		
Pit (10)	3	—	1	—	2	3[2]	—	—	—	—	—	—	1	—	—	—	—	3.70
Sprague (5)	4	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1.60
Crooked (9)	8	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.11
Total (24)	15	1	1	—	2	3	—	—	1	—	—	—	1	—	—	—	—	1.92
L. sp.																		
Willow (1)	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	3.0?
L. tridentata																		
Klamath (453)																		
Shasta R. (437)	76	51	117	64	98	13	11	5	2	—	—	—	—	—	—	—	—	2.410
Klamathon (15)	—	—	—	—	2	1	3	3	3	1	—	1	—	—	—	1	—	7.40
Copco L. (1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	16.0?

Table 6 (continued). Counts of posterior circumoral teeth in *Lampetra lethophaga* and in Klamath River precocious populations of *L. tridentata*

Species River system (No.)[1] Locality (No.)[1]	Total number of unicuspid posterior circumorals										
	1–2	3–4	5–6[2]	7–8	9–10	11–12	13–14	15–16	17–18	19–20	Mean[3]
L. lethophaga											
Pit (10)	1	—	2	1	3	1	2	—	—	—	8.90
Sprague (5)	—	—	—	1	1	2	1	—	—	—	10.80
Crooked (8)	—	—	—	—	2	4	2	—	—	—	11.25
Total (23)	1	—	2	2	6	7	5	—	—	—	10.73
L. sp.											
Willow (1)	—	—	—	—	—	—	1	—	—	—	14.0?
L. tridentata											
Klamath (453)											
Shasta R. (437)	—	—	—	—	5	14	94	174	130	20	15.657
Klamathon (15)	1	—	—	1	4	6	2	1	—	—	10.60
Copco L. (1)	—	1	—	—	—	—	—	—	—	—	3.0?

[1]Number of specimens.
[2]Value for holotype; the holotype has 6 unicuspid posterior circumorals.
[3]Mean from uncombined data.

Table 7. Counts of oral papillae in all available adults of *Lampetra lethophaga*, in the adult of uncertain species from Willow Creek, and in the 14 countable specimens of *L. tridentata* from the Klamath River at Klamathon

	Papillae on each side			Anteromedian papillae			Total papillae		
	lethophaga	Species?	*tridentata*	*lethophaga*	Species?	*tridentata*	*lethophaga*	Species?	*tridentata*
Number of counts	58	2	30	29	1	15	29	1	15
Range of counts	2–13	6–6	6–12	0–2	1	1–3	5–26	15	14–26
Mean of counts	7.7	6?	8.6	1.03	1?	1.20	16.3	15?	18.5

pertinence), though the counts for the nonparasitic form may be slightly the more variable and slightly the lower on the average, because of some low-count variants.

MYOMERES

The myomeres were counted, as recommended by Hubbs and Trautman (1937: 28), from the first segment that wholly (or almost wholly) lies behind the groove around the last gill-opening, to the one whose lower posterior angle lies in part or wholly above the cloacal slit.

The number, for both ammocetes and adults, has proved to be highly variable in *Lampetra lethophaga*, with a suggestion of some regional diversity, though with a broad overlap. For the three stream systems the counts follow:

Pit River (29 specimens): 63–69; mean 65.62±.31.

Sprague River (8): 58–66; mean 63.50±.94.

Crooked Creek (46): 63–73; mean 67.20±.29.

Bond (1961: 14) gave the number for ammocetes, presumably from Crooked Creek, as about 65–70. Ting T. Kan (pers. comm., 1970) counted 63–69 (mean 65.71±.16) in 95 ammocetes from Crooked Creek, in part overlapping the specimens I have counted.

These numbers roughly approximate, in mean value, those found for *Lampetra tridentata*, in which, however, there is much regional variation in this character. On the basis of myomere counts Creaser and Hubbs (1922: 6) erroneously separated that species into two subspecies: "*Entosphenus t. tridentatus*" from Unalaska to the Columbia River, with 68 – 74, and "*E. t. ciliatus*," from southern Oregon to southern California, with 57 – 67 myomeres. For a series from Coyote Creek in central California, however, Hubbs (1925: 592) gave the range as 67 – 76, and Hubbs (1967: 307) listed 60 – 70 for 5 specimens from southern California and from off northwestern Baja California. Other, unpublished, counts have mostly approximated 70.

PROPORTIONAL MEASUREMENTS

The proportional measurements (Table 8) of body parts (expressed as permillage of total length) are fairly consistent among the adults referred to *L. lethophaga* from the different stream systems, but are in part somewhat different from the values for the dwarf Klamath River stocks of *L. tridentata*. Outstandingly different is the size of the oral disc, which, as would be expected, is the smaller in the nonparasitic form (36–49 *vs*. 74–96); the Willow Creek form (of uncertain species) is strikingly intermediate (64). A similar relation, as to be expected, holds for the snout length, though with some overlap. Little difference is indicated for eye length of adults, except that the eye is largest in the Willow Creek specimen. Length over gill-pores seems to average only slightly lower in *L. lethophaga* than in the Klamath precocious stocks of *L. tridentata;* the value for the Willow Creek example is a bit higher than the average for the *L. tridentata* series. Virtually the same relation holds for body depth, again with much overlap. The tail, also with much overlap, averages longer in the *L. lethophaga* than in the *L. tridentata* series, but is distinctly longer in the Willow Creek specimen.

Measurements of ammocetes and transformers as well as adults of *L. lethophaga* indicate some average ontogenetic changes in body proportions. Consistent differences with age and stage, however, are not clearly shown for the tail length. As is usual in lampreys, the body depth increases and the point of greatest depth shifts from near the last gill-slit to just before the origin of the dorsal fin. The distance over the gill-pore series is shorter in the transformers and in the adults than in the ammocetes. The eye, snout, and length over gill-pores appear to average proportionately larger in adults than in transformers.

Table 8. Measurements in permillage of total length of *Lampetra lethophaga* and of Klamath River precocious populations of *L. tridentata*. Mean values in parentheses

Stage / Species / River system (No.)	Tail length	Body depth	Over gill-pores	Eye length	Snout length	Disc length
Ammocetes (over 100 mm)						
L. lethophaga						
Pit (3)	282–295(290)	56–63(60)	91–132(112)	—	—	—
Sprague (2)	314–322(318)	58–62(60)	121–125(123)	—	—	—
Crooked (33)	252–319(297)	51–68(61)	97–137(111)	—	—	—
Transformers						
L. lethophaga						
Pit (20)	294–343(309)	57–72(64)	82–107(94)	12-20(16)	40–62(51)	23–47(37)
Adults (maturing to mature)						
L. lethophaga						
Pit (11)						
Holotype	282	63	92	18	64	42
All types	272–323(297)	59–86(68)	81–104(96)	18–22(20)	61–78(68)	36–51(45)
Sprague (5)	300–326(306)	60–80(70)	89–110(98)	16–24(20)	62–88(73)	43–56(47)
Crooked (13)	255–328(301)	66–86(74)	88–108(100)	15–21(18)	65–94(80)	42–58(49)
Total (29)	255–328(300)	59–86(71)	81–110(98)	15–24(19)	61–94(74)	36–58(47)
L. sp.?						
Willow (1)	341	76	108	24	93	64
L. tridentata						
Klamath (16)	270–300(282)	75–91(83)	93–122(103)	17–20(18)	86–112(99)	74–96(81)

In his key to the lampreys of Oregon, Bond (1961: 14) entered "body rather stout and deep" for *L. lethophaga* (his "*Lampetra* sp."), which would suggest a contrast with *L. tridentata,* though he included no alternative for the parasitic species. He had, I assume, adults of *L. lethophaga* only from Crooked Creek, where the mature specimens exhibit nuptial features, with the body often turgid, whereas in general *L. lethophaga* is much slenderer than the precocious populations of *L. tridentata* in the Klamath River system. Other contrasting characters assigned by Bond presumably reflect the nuptial modifications of *L. lethophaga* in Crooked Creek.

COLOR

Life colors were annotated in the field on maturing to mature adults, comprising the male and female type specimens (UMMZ 130648 and 130649) from Fall River (Location 2), and on one maturing male (UMMZ 130576) from Sprague River opposite Ferguson Butte (Location 7); collected respectively on August 17 and August 10, 1934. Three types taken in vegetation displayed only a trace of the silvery color of macrophthalmiae. They were slaty above to bright brassy-silvery below. The fins were clear waxy-yellow. Of those taken under a stone, the males seemed to approach the silvery color typical of macrophthalmiae more than did the females. The one male from Sprague River, taken in dense vegetation, was deep purplish-brown above the lighter belly, and showed no trace of the silvery phase.

Preserved adults not in full nuptial condition, whether early in development or of stocks that do not attain typical nuptial characters, are dusky purplish over most of the surface, becoming pale yellowish on lower surfaces of head and trunk and on the ventral fin fold behind the anus; the mid-dorsal ridge is weakly lighter; and the second dorsal is dusky on the extreme base only. Specimens in full nuptial development are blackish-purple on the darker areas and on the basal part of both dorsal fins, and the region about the cloaca is conspicuously paler.

The caudal fin in adults is variably darkened, but is generally darkest along the edges of the muscle mass and often lighter near the edge. In high-nuptial adults the caudal area becomes very deeply pigmented, and is almost black along a basal strip, especially on the lower side.

Younger ammocetes are almost uniformly darkened, barely lighter below. The caudal fin is at first largely clear, except in the narrow dark streak margining the muscle mass, about equally above and below. With increasing size the caudal fins grow darker, progressively outward, as the lighter margin becomes narrow. At any stage, however, the paler border varies much in width and intensity, as does the basal dark streak. Occasionally, a submedian dark streak develops on either lobe, and the dark area may be blotched.

Transformers are rather evenly pigmented, and the caudal area is largely dark, with the paler border and the dusky basal streaks varying much in width and intensity. Recently transformed specimens contrast sharply with those of *L. tridentata,* including the precocious Klamath types, in color, in the same way that the macrophthalmiae of *L. fluviatilis* and *L. planeri* differ (Hardisty, Potter, and Sturge, 1970: 385, pl. 1).

At all stages the pigment in the caudal fin area is often marked along the axial line by small dusky blotches, from which close-set and very oblique melanophore files extend across the muscle mass, above and below, margining the myomeres.

All of the color features, and in the stated variation, as described above, were seen in both ammocete and adult stages of the parasitic stocks of the Klamath River system, and elsewhere. Therefore, I fail to confirm any pigmentary differentiation that may be implied in the statements, in the key to Oregon lampreys by Bond (1961: 14), that the ammocetes of the nonparasitic form that he designated "*Lampetra* sp." have "dark pigmentation outlining tip of tail," and that the larvae of *L. tridentata* have "a dark line above and below tip of tail."

Vladykov (1950, 1960) described in detail sharp pigmentary differences at various ammocete stages between *Lampetra lamottenii* (Leseuer) and *Petromyzon marinus,* but J. R. Nursall and D. G. Buchwald (pers. comm., 1970) have found that *Lampetra lamottenii* in this respect agrees essentially with the closely related parasitic *L. japonica.*

LIFE HISTORY TYPE

An outstanding reason for the interpretation of *Lampetra lethophaga* as a distinct species of the *Entosphenus* complex is its alignment among the nonparasitic lampreys, which have traditionally been accorded specific rank.

It is now recognized that nonparasitic forms have repeatedly evolved from parasitic lampreys. The original discovery, now well analyzed, was that of *Lampetra fluviatilis* (Linnaeus) and *L. planeri* (Bloch), and a parallel case involving Pacific forms of the subgenus *Lampetra* has been documented (Vladykov and Follett, 1965). A few parasitic/nonparasitic pairs were implicit in the revision of northern lampreys by Creaser and Hubbs (1922) and the repeated origin of nonparasitic forms from parasitic ones was definitely indicated by Hubbs (1925) for northern lampreys in general and by Hubbs and Trautman (1937) for three separate lines within the genus *Ichthyomyzon,* one of which had been treated earlier (Reighard and Cummins, 1916); the dual origin of nonparasitic forms from one parasitic species in this genus was indicated by Raney (1952). The speciational aspect of the repeated origin of nonparasitism in lampreys was mentioned by Hubbs (1940: 203; 1941: 188 – 189). Other authors, in particular Zanandrea (1951 – 1962) treated and expanded on the problem of "paired species of lampreys." Alvarez del Villar (1966) discovered the nonparasitic *Tetrapleurodon* of Mexico, and Potter (1968, 1970; Potter, Lanzing, and Strahan, 1968; Potter and Strahan, 1968) described, as a full species, the nonparasitic form of the Southern Hemisphere genus *Mordacia.* Hardisty (1963, 1969) and others have also dealt with this problem. The systematic status and frequency of the "paired species" is being discussed by Hubbs and Potter (in press) and the biological interrelations are being treated by Hardisty, Potter, and Sturge (in press).

Lampetra lethophaga parallels the other nonparasitic lampreys in the rapid maturing of the gonads, which attain full maturity soon after metamorphosis. No difficulty is experienced in sexing either transformers or early-stage adults. As usual in fishes the testis at comparable early stages can be distinguished from the ovary by the circumstance that it is a slenderer, thinner, whiter, and more opaque band. The testis of this lamprey was observed to become markedly lobular as it rapidly enlarges during metamorphosis. The penis at full maturity remains small (Figure 2A). In the holotype, the penis does not extrude.

When *Lampetra lethophaga* was first encountered in August, 1934, and for a long time thereafter, no doubt was felt regarding its interpretation as a nonparasitic species, the first to be recognized in *Entosphenus.* The discovery of the Miller Lake lamprey, a reportedly even more dwarfed yet parasitic form of the same complex, however, has called for a more thorough appraisal of the evidence for the elimination of feeding by the adults of *L. lethophaga.*

Not one of the considerable series of adults of *L. lethophaga,* taken throughout much of the year (Table 1) and representing a full range of stages in maturity was found to contain any food in the gut. A few had the intestinal wall darkened by apparent hemorrhage and a few had lumps of some material in the gut, but these appeared to be cysts and indeed one when opened discharged a larval nematode. Nor did any of the 114 transformers from Hat Creek (Location 3), collected on October 4, 1968, show signs of having eaten.

Ammocetes longer than about 100 mm, taken May 3–16, June 26–27, August 13–17, September 4, and October 4–20, showed that early stages in the maturing of the gonads are represented through this long period (Table 1). Transformers, taken on September 4 (one specimen) and on October 4 (114) show that the gonads undergo further maturing in that stage: the ova in many of these specimens, even before the elaboration and cornification of the teeth, were estimated, by visual inspection, to be from one-fourth to one-half full size, and to be far fewer than in the dwarfed parasitic form of the Klamath system. Bare traces were observed of the postmetamorphic macrophthalmia stage (characterized by much enlarged eyes and silvery color), such as is prominently shown by the parasitic populations of *L. tridentata,* both dwarfed and full-sized. The incipient macrophthalmiae of *L. lethophaga* contrast with the typical macrophthalmiae of *L. tridentata* just as do the corresponding stages of *L. fluviatilis* and *L. planeri,* as well depicted by Hardisty, Potter, and Sturge (1970: 385, pl. 1).

All adults taken from February 16 to August 17 (Table 1) have gonads in various stages from early to full maturity, though they are, with only moderate overlap, smaller than the transformers (Figure 8). The smaller size of the adults presumably resulted from the actual shrinkage that is known to occur in lampreys during transformation, with, in the case of nonparasitic forms, no later resumption of growth. However, the transformers and the adults did not come from the same place.

Pertinent testimony was secured from the personnel of the Klamath State Fish Hatchery on Crooked Creek (Location 11), where several series of this lamprey were collected at various times of the year. On August 13, 1934, the superintendent of the hatchery informed me that considerable numbers of small lampreys about 5 – 8 inches long which are removed from the screens of the hatchery ponds each year about June contain eggs "about the size of whitefish eggs, showing through the belly along almost the entire length of the body." He added that there are definitely no "runs of eels" in this or in other, nearby streams. On February 5, 1945, the late Dr. Paul R. Needham reported (pers. comm.) that the superintendent had not seen any of the lampreys. On recent occasions the hatchery employees have provided Dr. Carl E. Bond (pers. comm., 1970) with corroborative testimony.

Fish management studies on lower Hat Creek (Location 3) have led Dr. Roger A. Barnhart (pers. comm., 1970) to conclude that the lamprey of that stream is a nonparasitic "brook" form. Nor have I found any evidence of parasitic lampreys in the drainage basins of Pit, Sprague, or Sycan rivers, or in Crooked Creek, from which the material of *Lampetra lethophaga* was obtained.

SEX RATIO

By gross examination it was readily feasible to ascertain the sex ratio of ammocetes larger than 90 mm total length and of all transformers, as well as the adults. The sex of some ammocetes and a few of the transformers of earliest stage was not listed until a small piece of the gonad had been teased apart or crushed between slides, so as to distinguish the testicular tubules from early ova. For only two of the 115 transformers examined was any hesitation encountered in the sexing.

For all 187 specimens sexed, of all stages, the females were moderately outnumbered by the males 87:100. The ratio of females per 100 males seems to decrease with the stage of development: from 128 for 23 female and 18 male ammocetes longer than 90 mm, through 79 for 51 female and 64 male transformers, to 72 for 13 female and 18 male adults. The significance of this indicated change in sex ratio, and indeed its validity, call for further study. Marked fluctuations have been indicated for the sex ratio of *Lampetra planeri*

(Hardisty, 1944, 1954; Zanandrea, 1951). A preponderance of males has been found for *Petromyzon* (Applegate, 1950, App. E).

ETYMOLOGY

The name *lethophaga,* figuratively referring to the elimination of feeding as adult, is formed by combining the latinized expressions *leth-,* from the root of $\lambda\eta\theta\eta$, a forgetting or forgetfulness; the normal connective *-o-* in words of Greek origin; *phag-,* from the root of $\phi\alpha\gamma\varepsilon\iota\nu$, to eat; and *-a,* from the feminine of the adjectival suffix -ος.

RELATION OF NONPARASITIC *LAMPETRA LETHOPHAGA* TO DWARFED PRECOCIOUS PARASITIC FORMS REFERRED TO *LAMPETRA TRIDENTATA*

Although Hardisty and Potter (in press) hold to the opinion that the genes do not interflow between the members of the respective parasitic/nonparasitic pairs, some indications have been emerging that within several of the "paired species" of lampreys the typical large parasitic form may to some degree intergrade with its dwarfed nonparasitic representative. Intermediacy in size is indeed shown by the "praecox" forms in several species, such as have been discussed by Berg (1931, 1948, 1962) and others. The reduction in size is thought to be due to a shortening of the parasitic cycle, which is also a sign of intermediacy. The high frequency of the "paired species" (Hubbs and Potter, in press) strongly suggests speciational plasticity, and begets the idea that nonparasitic populations may be polyphyletic even within any species complex.

There have even been some suggestions that the nonparasitic types should be accorded only subspecific status. Thus, it has been proposed (Hubbs and Lagler, 1958: 36–37; 1964: 36–37) that the American brook lamprey be distinguished only subspecifically as *Entosphenus lamottenii lamottenii,* since "in Alaska it appears to intergrade with the typical, often anadromous parasitic form *japonicus.*" This action, although drawing some support from studies by Heard (1966) and by J. R. Nursall and D. G. Buchwald (pers. comm.), was probably premature, but the problem of systematics within the *Lethenteron* group (now probably best treated, along with *Entosphenus,* as a subgenus of *Lampetra*), is definitely open. In some recent studies difficulty has been encountered in the identification of certain specimens of *Ichthyomyzon,* where *I. bdellium* (Jordan) and *I. greeleyi* Hubbs and Trautman are sympatric (Ernest A. Lachner, pers. comm., 1971). However, for the present at least, it seems advisable on both practical and theoretical grounds to maintain the nonparasitic forms at the full specific level.

Suggestions that the parasitic and nonparasitic representatives may intergrade stem in considerable force from studies of the *Entosphenus* complex in the related drainage basins of the Pit and Klamath rivers, from which the nonparasitic form is herein being made known. Indeed, intermediacy between the two trophically contrasting types was probably first suggested (Hubbs, 1925: 589, fig. 16) for populations of *"Entosphenus tridentatus"* in these two river systems. A race of this species in Goose Lake of the Pit River system was shown as straddling the intervening line on the chart, on the basis of an examination of material in the United States National Museum collected by Barton Warren Evermann, and it was stated that: "Of a series of small adults, all taken on trout in this lake, the *males* showed a decided approach toward the brook type of lamprey in the close approximation of the dorsal fins, relatively blunt teeth, atrophy of the intestine and precocious sexual development. The *females,* oddly, were not so altered, but resembled the normal parasitic young of the species." It was added that "Some specimens from Klamath Lake, not far distant from Goose Lake, but in a distinct stream system, also show evidence of degeneration." I may have been dealing, however, merely with stocks in these lakes that were maturing at a small size, perhaps particularly as males, and were assuming the nuptial characteristics that may be essentially similar in the two trophic types.

I have found other evidence of the existence in the Klamath River system of a presumably indigenous and landlocked local form (or of forms) intermediate in size between the large sea-run *Lampetra tridentata* and the endemic nonparasitic dwarf, *L. lethophaga.* Indeed, as is indicated below, there is reported to have been, in Miller Lake, an isolated parasitic form at least as small as *L. lethophaga.*

Fifteen maturing adults only 214–274 mm long, no doubt at approximately the maximum size they would have attained, from Klamath River at Klamathon, have been studied. These specimens (SU 28783 and 35555) were collected at a fishery research installation, respectively by E. A. McGregor, in the fall of 1922, and by Charles H. Gilbert (who died in 1928). They are distinctive in the high number of cusps on the teeth. In this respect they resemble a series of 374 specimens in the macrophthalmia (early-transformation) stage taken nearby, on February 24 to April 5, 1931, in Shasta River at its junction with the Klamath, in wiers set across the stream to tally downstream salmon migrants (Brown, 1938). Tooth and cusp counts taken on all specimens of both lots are herein tabulated, along with those of *Lampetra lethophaga* (Tables 3 – 6) as these lots are taken to represent or to approximate the ancestral form of *L. tridentata* from which the nonparasitic species originated. The counts for these two lots of *L. tridentata* are in fair agreement, with the unexplained exception that the Klamathon series yielded much the higher counts of bicuspid posterior circumoral teeth. This discrepancy seems particularly strange, when it is noted that the two series were taken only about 11 km apart.

Stranger yet are the characters of a single specimen, even more deviant than those of the Klamathon series. It was taken from Copco Lake, only about 18 straight-line kilometers farther upstream, near the Oregon state line. This specimen, CAS 25987, collected by Millard H. Coots, was adhering to the tongue of a sucker, *Catostomus rimiculus,* that had been caught in a gill-net set overnight, June 3–4, 1953. It is a subadult female, with the gut turgid with food and with the enlarging ova too few for the large sea-run type. It is 241 mm long, about as large as the Klamathon specimens, and its permillage measurements are included within the range for the Klamathon series in Table 8, but the dentition is sharply divergent: in particular, the total number of bicuspid posterior circumorals (16) is higher than in any of the 452 other specimens of *L. tridentata* tallied (Table 6), and some other counts are aberrant. The dentition of this specimen is as follows: longitudinal lingual cusps 29 – 29 = 58 (high); anterior lingual cusps 12 + 1 + 13 = 26 (high); supraoral cusps 3 (normal); infraoral cusps 6 (aberrantly high); anterior circumorals 5 (usual); lateral circumorals 2 – 3 – 3 – 2 — 2 – 3 – 3 – 2 (normal); posterior circumorals 19 (very high) with 16 bicuspid (absolutely extreme) and only 3 unicuspid (next to lowest number; the seventh, tenth, and eleventh of the 19 teeth beginning with the anteriormost and foremost on the right side); 2 marginals on each side greatly dilated; total marginals 57; total teeth 104 (high); total cusps 220 (exceptionally high). Oral papillae 12 + 1 + 9 = 22 (high).

The differences between the lampreys comprising the Shasta River, Klamathon, and Copco Lake series exemplify the tendency toward high local variability of resident lampreys, on a mosaic pattern. Small wonder that *Lampetra lethophaga* displays some local differences.

Additional material of the "praecox" type of *L. tridentata* from the Klamath River and other systems, particularly from Goose and Klamath lakes, are currently under study by Dr. Carl E. Bond of Oregon State College and his graduate student Ting T. Kan. More or less comparable precociously spawning forms now referable to *L. tridentata* have come to my attention from southern California (Hubbs, 1967) and northward to Vancouver Island, British Columbia. Dwarf, nonmigratory races have been discussed by McPhail and Lindsey (1970: 58–59). There appear to be numerous forms that seem to be comparable to the races of salmon of diverse and distinctive size at maturity (in each case just before reproduction and death).

Limited material at hand from the drainage basins of Clear Lake and of Lost River, in the Klamath system, may bear on the problem of possible intergradation of parasitic and nonparasitic representatives of the *Entosphenus* group. This is particularly true of a single specimen, a postnuptial male only 176 mm in total length (SIO 65 – 144) that was collected by William Johnson and Edward J. O'Neill on May 13, 1965 in Willow Creek, tributary to Clear Lake, Modoc County, California. Originally, as shown on the one-degree 1:250,000 U.S.G.S. Modoc Lava-Bed Sheet of 1892, and on the accompanying distribution map (Figure 3), Willow Creek was the upper, southern headwater of Lost River, of the Klamath River upstream complex, but with an intermittent, presumably flood inflow into Clear Lake. Currently, the flow is directed into this lake, which thus has been enlarged as a reservoir. This specimen was first regarded as referable to *Lampetra lethophaga,* then was thought to represent, more likely, a greatly dwarfed parasitic race. A third possibility, suggested by some recent testimony, is that the specimen in question is merely an exceptionally dwarfed example of a moderately dwarfed resident population. Mr. O'Neill has informed me (pers. comm., 1971) that a number of lampreys 10–12 inches long have been taken adhering to crappies (*Pomoxis* sp.) in Willow Creek, and that many of the "rough fish" of this stream have shown lamprey scars.

Neither by tooth and cusp counts (entered on Tables 3–6 in the row labelled "*L.* sp."), nor by other characters, have I found it feasible to decide to which of these possibilities this Willow Creek fish can be assigned. In general, such postnuptial specimens are often difficult to refer to trophic type. On comparison with *L. lethophaga* and the precocious Klamath forms of *L. tridentata* this particular specimen is conspicuously intermediate in several respects, as follows:

The Willow Creek specimen (Figures 2 C, D) is definitely smaller than any known mature parasitic adult from the Klamath River system, or elsewhere (other than the representatives mentioned below of the tiny parasitic form of Miller Lake, a disjunct part of the Klamath basin); yet is 16 mm longer than the largest transformed adult at hand of *L. lethophaga* (Figure 8). It is 23 mm shorter than the largest specimen in transformation, but lampreys shrink considerably during and just after metamorphosis.

Particularly notable for the trophic indication is the measurement of the buccal disc (Table 8), which is intermediate, without overlap: 64 thousandths of the total length, *vs.* 36 – 58 (mean 47) for *L. lethophaga* and 74 – 96 (81) for the *L. tridentata* series. The correlated snout length is also definitely intermediate, but with slight overlap. Body depth is probably also intermediate, but tail length and eye length are higher than in either type under comparison, and length over gill-pores is likely also high (Table 8).

The regular formulae for the cusps on the two oral teeth (supraoral 3 and infraoral 5) and for the four lateral circumorals of either side (2 – 3 – 3 – 2) tend to align the Willow Creek specimen with the parasitic type (Tables 3, 4). Furthermore, the teeth are rather less degenerate than in breeding examples of *L. lethophaga,* and the median cusp on the supraoral is relatively large and sharp, instead of being reduced or absent as it usually is in the nonparasitic form. The total count of posterior circumoral teeth, however, seems intermediate: 2 higher than any count for *L. lethophaga* and on the low side for the parasitic lampreys from Klamath River (Table 6).

The general appearance of the Willow Creek specimen approximates that of the mature adults of *L. lethophaga* from Crooked Creek, so much so as to suggest consanguinity: in each the color is dark, the entire face is strongly turgid, the whole form is robust, the dorsal fins are much expanded and in contact, and their edges are minutely frayed. However, the similarities may largely reflect a similar stage in sexual development.

In conclusion, it does not seem justified to align the Willow Creek specimen with either *L. lethophaga* or with the Klamath River precocious populations of *L. tridentata*. Its general intermediacy, along with some extreme features, indicate it to be a representative of a somewhat distinct local form.

Data possibly bearing on the uncertain status of the Willow Creek lamprey are furnished by two specimens taken on June 24, 1965 by Edward J. O'Neill and James Keith on the Clear Lake National Wildlife Refuge, during banding of White Pelicans. They were among 44 lampreys spewed up by one young pelican. These may have been captured by the parent(s) in Clear Lake (now used as a reservoir and a refuge), but may have come from elsewhere, as White Pelicans sometimes forage many miles from their rookery. Whatever their source, these 2 specimens, although very considerably damaged, seem to represent a stock different from that of the one Willow Creek specimen. They are larger: one not sexable measures about 220 mm in total length and the other, a female with nearly ripe ova, about 240 mm, *vs.* 176 mm. Permillage proportions, though hardly precise, seem to differ: tail length, 317 and 327 *vs.* 340; eye length 15 and 17 *vs.* 24; snout length 73 and 86 *vs.* 93. Teeth and cusps number: transverse lingual cusps, 12 + 1 + 12 and 12 + 1 + 14 (higher than in *L. lethophaga*); cusps on supraoral 3 and on infraoral 5 in each, as usual; posterior circumorals 16, apparently all unicuspid. Clearly these two specimens seem to represent a dwarfed population of parasitic lamprey, probably similar to the precocious type sampled from the Klamath River near Klamathon and perhaps similar to the form or forms occurring in Shasta River and the Klamath lakes.

The most surprising circumstance bearing on the relationship between *Lampetra lethophaga* and the parasitic forms referred to *L. tridentata* is the discovery by Dr. Carl E. Bond of a parasitic form indicated as even smaller than *L. lethophaga*. This form seems to have been endemic in the small drainage basin (shown on the distribution map, Figure 3) of Miller Lake (named Fish Lake on some old maps), which basin is a disjunct, endorheic unit, ending in a marsh, at the north end of the Klamath drainage system. Dr. Bond has stated (pers. comm., 1971) that:

> The evidence for predation in the Miller Lake lamprey is strong. The little beasts prevented the maintenance of a trout fishery in the lake. They would kill trout and tui chub [*Gila bicolor*] and then mine out the soft parts, leaving the perforated skin and the skeleton on the bottom. Spawned-out lampreys were also devoured — even on the spawning beds. Miller Lake is in T 27 S, R 6½ E, Sections 11 – 14 and in a distrupted portion of the Klamath River drainage.
>
> The lamprey is now extinct, a [tragic] victim of a toxaphene operation designed by the Oregon State Commission to eradicate it. I had hoped that it had survived in the outlet, Miller Creek, but no specimens were taken there through extensive and thorough electrofishing by Harry Lorz of the Oregon State Game Commission in 1970, many years after the extinction of the lamprey.
>
> Adults from the spawning beds range from 72 to 129 mm, mostly between 80 and 105 mm. Many of the near-term ammocetes and some of the non-spawning adults are longer than the spawning adults. Some of the lampreys spawned in the very cold creeks that are tributary to Miller Lake, but the major spawning areas were along the lake shore.
>
> I have thought much during the past 15 years about the significance of the Miller Lake lamprey as a transitional form in a progression to nonparasitic habits. The creatures were locked into a system with only the tui chub, if indeed the chub was not planted later, and had adapted to the paucity of food by cutting a year or two off their lives, so that they metamorphosed in the fall and spawned in the spring and summer — feeding fiercely if food were available, but not growing beyond the length of the ammocoetes. Even when the Game Commission planted trout yearly the lampreys did not grow beyond the range I mentioned — although the trout plants were wiped out each winter.
>
> To me, the outstanding attribute of this form is that parasitism was not obligatory and that the population finally consisted of the offspring of ancestors that could feed fiercely if prey were on hand, but apparently could mature and spawn on a starvation diet. I suspect that if any native fish other than the lampreys were in Miller Lake, the populations were kept low by the lampreys — much as in the same

manner that hatchery plants of trout were virtually wiped out. One year class could feast to the extent that the next would have little or nothing to eat, unless the Game Commission planted more trout.

The alternative name of Fish Lake, found on various old maps, suggests that the tui chub was probably a native associate of the Miller Lake lamprey.

A detailed comparison of *L. lethophaga* with this parasitic midget awaits the completion of the study by Dr. Bond and Mr. Kan.

Clearly these data on the small lampreys of the Klamath River system are pertinent not only to their systematic appraisal, but also to the general problem of the relationships between parasitic forms of lampreys and their nonparasitic relatives, probable derivative. It is certainly conceivable that the two types do in some way intergrade, with or without active exchange of genes, and the strong possibility remains that some or even all of the nonparasitic types may be polyphyletic.

GROWTH

Data are inadequate to indicate clearly the life span of the ammocetes of *Lampetra lethophaga* but it appears probable that the period is at least four years (Figure 8) — comparable to the evidence for other lampreys (Loman, 1912; Meek, 1916; Okkelberg, 1921, 1922; Hubbs, 1925; Schultz, 1930; Ivanova-Berg, 1931; Leach, 1940; Knowles, 1941; Hardisty, 1944 – 1969; Churchill, 1947; Applegate, 1950; Horn and Bailey, 1952; Dendy and Scott, 1953; Seversmith, 1953; Zanandrea, 1951, 1954b; Hardisty and Potter, in press). In addition, I have unpublished, original, confirmatory observations for *Petromyzon marinus* Linnaeus, *Okkelbergia aepyptera* (Kirtland), *Lampetra tridentata*, and *L. lamottenii*. The graph for *L. lethophaga* (Figure 8) covers all localities and all dates, but most ammocetes measured were collected in August (40) and October (95); only 17 others were taken over the time span of May 3 to September 4. The sharp mode at 20 – 29 mm length presumably represents young-of-the-year, all of which were collected on August 13 (Table 1). The four modal size classes in the total-length range of 90 – 129 mm obviously represent at least one older year-class. The intervening size classes likely represent another. On the basis of life-history studies of other lampreys, it is highly probable that the 7 ammocetes longer than 159 mm, all taken on October 20, would have undergone another year of larval life.

The time of metamorphosis from the ammocete stage is adequately indicated only for the large collection of 114 individuals in early to late stage of transformation taken on October 4, 1968, by poison in Hat Creek near its mouth into Pit River, at Location 3. The only other transformer examined was the specimen taken on September 4, 1898 in the North (or South) Fork of Pit River, at Location 1 (Table 1).

Entosphenus tridentatus, as well as other lampreys, probably also metamorphoses in the fall. Along with a large sample of ammocetes of that species taken in Trinity River at Lewiston, California, on November 8, 1945, are 2 males and 2 females in a late stage of transformation, but with the teeth remaining in pads or only partly and variably exposed. These transformers are 102, 106, 108, and 115 mm long, within the dominant size classes of the macrophthalmiae taken either at the same place, or in the lower Shasta River (Figure 8).

The size frequencies of the transformers of *L. lethophaga* form a normal curve (Figure 8), which lies almost entirely higher than the sizes of either the transformed and transforming examples, just cited, or the precocious Klamath River type of *L. tridentata*. An incompletely transformed specimen from Coyote Creek, at San Jose, California, was listed as of intermediate size, 141 mm, by Hubbs (1925: 594). It has been shown that nonparasitic lampreys metamorphose at a larger size than do their larger, parasitic relatives. This relation has been so stated for the paired species of *Mordacia* (Potter, 1970: 497) and is being indicated as a generalization by Hubbs and Potter (in press) and by

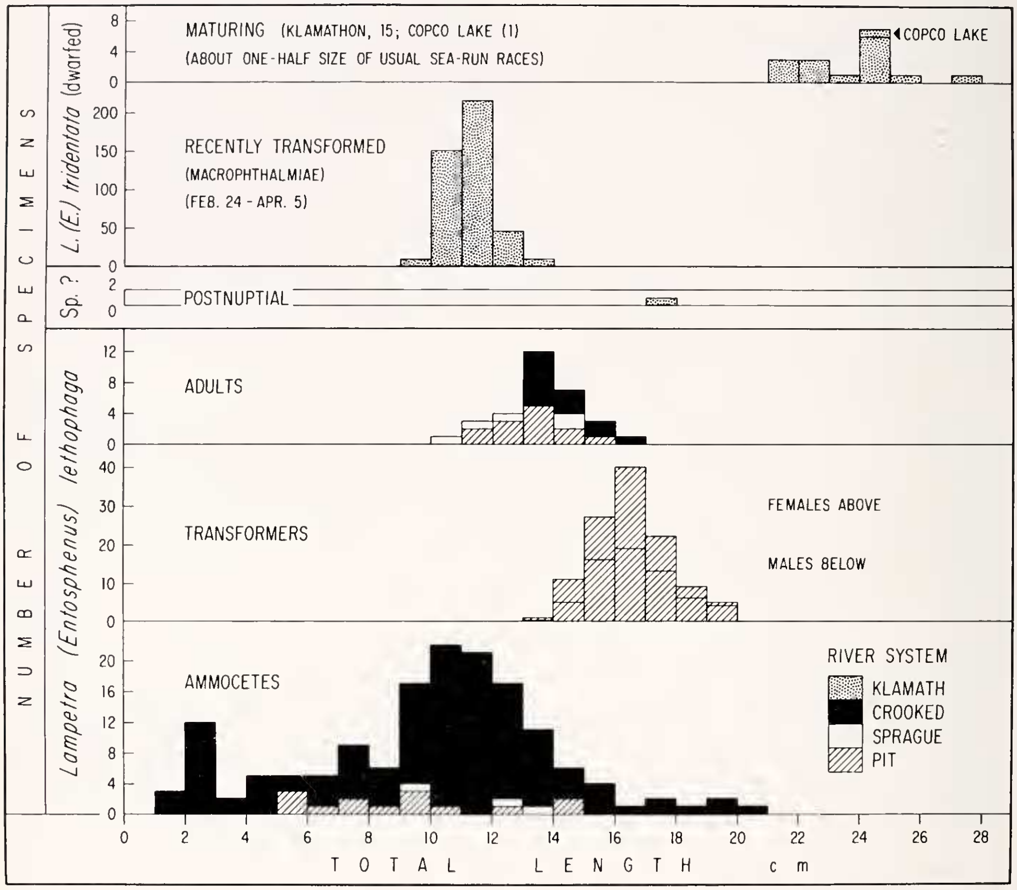

Figure 8. Total-length measurements of all material studied of the nonparasitic *Lampetra lethophaga*, of the specimen (*L.* sp.) of doubtful pertinence from Willow Creek, and of the parasitic, but praecox, form of *L. tridentata*, from Klamath River. The measurements were made to the nearest mm, but are grouped by cm (10–19, 20 29, etc.). Number of specimens shown on ordinate.

Hardisty and Potter (in press).

In concordance with other evidence of size shrinkage during metamorphosis in lampreys, perhaps particularly in nonparasitic species, the modal size of the transformers seems lower than the size of the largest ammocetes, which are the only ones that could be expected to metamorphose. However, the ammocetes and the transformers were not taken at the same locality.

It is probably also significant, and in line with expectation for a nonparasitic lamprey, that the postmetamorphic, maturing and mature adults of *L. lethophaga* are, with little overlap, smaller than the transformers of the same species, but are, to a comparable extent, larger than the recently transformed macrophthalmiae of the lower Shasta Creek population of the parasitic *L. tridentata* (Figure 8). It has been observed for several lampreys that growth during transformation is negative.

It appears (Table 1) either that the time of breeding is unusually variable in *Lampetra lethophaga*, or that full sexual development may be long delayed. Specimens taken in

Crooked Creek (Location 11) and in a spring near Sprague River (Location 10), the only ones exhibiting definite nuptial modification, obviously had spawned, or would have spawned, in late winter or spring, for they were collected from February 16 to April 6 (Table 1). The other adults, at least some seemingly neotenic (see next section), were collected over the summer, from June 2 to August 17. The 11 adult types, taken on August 17 at Location 2, exhibited a wide variation in maturation, thus suggesting prolonged spawning unusually late in the year, or possibly a partial or even complete suspension of sexual development over the next winter. The single adults taken at five locations from June 2 to August 10 also varied widely in degree of maturation, further suggesting prolonged sqawning over the summer.

The great difference between the growth patterns of two resident types in the Pit-Klamath area is that *L. lethophaga* almost surely does not grow as adult, whereas the presumably resident, dwarfed forms of *L. tridentata* appear to double their size during their adult, parasitic life — even though they reach only about half the length attained by the larger sea-run populations of *L. tridentata.*

NEOTENY

Lampetra lethophaga exhibits, apparently in some populations only, definite indications of what may be considered as neoteny, other than that of merely reproducing soon after the postammocete metamorphosis.

The only specific reports of neoteny in a lamprey that I have found are by Zanandrea (1956, 1957a, 1958a, 1961) for the nonparasitic *Lampetra zanandreai* Vladykov. (This species is regarded by Hubbs and Potter (in press) as an isolated member, confined to the Po River drainage of Italy, of the subgenus *Lethenteron,* which has hitherto been regarded as restricted to the Arctic Ocean drainage from Europe to North America, to the North Pacific tributaries of Asia, and to northeastern North America.) Zanandrea (1961: 530) found at one locality 12 female ammocetes in an advanced ("third") stage of ovarian development, one of which "showed well-developed principal secondary sexual characters, namely, enlargement of the two dorsal fins, development of the anal pseudo-fin, and the transparent appearance of the body wall, through which the eggs can be seen . . . characters . . . normally associated only with adults that are about to spawn." He obtained at another locality other neotenic female ammocetes, constituting about one-fifth of a series of 221 in the larval stage. He suspected that neoteny in each place may have been induced by tannery pollution, but a test performed to check this suspicion was inconclusive.

The type of neoteny attributed to *L. lethophaga* involves the maturing at some locations of apparently all individuals of both sexes in the prenuptial condition. This is most strikingly shown by the adults from Fall River (the type station, at Location 2). They had passed through the ordinary, prejuvenile metamorphosis (transformation), but although some are in full maturity (witness a female turgid with large ova — Figure 1D), none has developed the ordinary nuptial attributes: melanistic pigmentation and the "principal secondary sexual characters" outlined above in the quotation from Zanandrea. These attributes are seen, well-developed, in 13 adults from Crooked Creek (Figure 2 A, B), in two males from the Sprague River system (Locality 10), in the specimen of uncertain species from Willow Creek (Figure 2 C, D), and in the 15 specimens, in early to late stages of maturing, of the dwarfed parasitic form (referred to *L. tridentata*) from Klamath River at Klamathon. These are the normal attributes of the nuptial stage of lampreys in general, attained at what may be called the second or nuptial metamorphosis. That transformation seems to have been elided at the head of Fall River (type locality of *L. lethophaga*), and is not evident in other specimens from the Pit River system. Series from the Klamath River complex other than at Locations 10 and 11 seem to be developing like the Fall River lot (maturity in prenuptial appearance). Therefore, the retention or elimination of the normal nuptial metamorphosis does not appear to provide a sound basis for the systematic distinction of nonparasitic lampreys of the Klamath complex from the Pit River form (typical *L. lethophaga*).

The stocks that are neotenic in the sense of developing without the usual nuptial attributes retain to a very large degree, through maturity, the features displayed in the late stages of the ordinary, prejuvenile metamorphosis. The body remains trim and non-turgid, and pale; the dorsal fins remain well separated, with at most a slight connecting ridge, and stay thin and non-turgid, low, and unfrilled at the margin; the other fins stay rather similar; even the anal is generally little enlarged, though moderately enlarged and turgid in the female shown in Figure 1D; the cloacal margins are little swollen; and the preanal fin fold is scarcely enlarged.

The neoteny was notably evident at the type locality (Location 2), where the water was cold (summer readings of 11.4–13.3° C), but the low temperature was presumably not a factor suppressing nuptial development because in Crooked Creek (Location 11), where the nuptial characters are well developed, the water was even colder (7.8° C in August).

REGIONAL DIVERSITY

There is considerable evidence of local diversity in *Lampetra lethophaga* other than the retention or loss of the nuptial metamorphosis, just discussed, but this observed diversity does not seem to warrant specific or subspecific distinction between the populations of the two main stream systems, or between populations within either system. In the analysis of variation the Crooked Creek population is contrasted with the populations sampled from the Sprague (including the Sycan) River system, both in the Klamath complex.

There seems to be some regional difference in the frequency of cusp number on the oral plates (Table 3). Loss of the median supraoral cusp is less frequent in Fall River specimens (the only fully adult ones from the Pit River system) than in those from Crooked Creek, but the few examples from the Sprague River system are intermediate. Some increase in number of infraoral cusps beyond the *Entophenus* standard of 5 was found in material from Crooked Creek and the Sprague River system, but not in the Fall River specimens.

There appear to be differences between the samples from the three stream systems in the frequency of reduction in cusp number on the four lateral circumorals from the typical *Entosphenus* pattern of 2–3–3–2 (Table 4). The frequency of bicuspid posterior circumorals runs higher in the Pit River sample than in the Crooked Creek specimens, whether tallied by individual teeth numbered from the side (Table 5) or by total number (Table 6), and again the specimens from the Sprague River system seem intermediate.

There may be average differences in number of trunk myomeres: lowest in the Sprague River system, highest in Crooked Creek, intermediate in the Pit River system.

There are some indicated average differences in proportional measurements (Table 8). In the larger ammocetes tail length and length over the gill-pores average longest for the Sprague River specimens, but only 2 are available. Very slight differences among the adults may be related to the expression of nuptial features in 2 of the 5 adults from the Sprague River system and in all 13 adults from Crooked Creek.

The more or less definite indications of local diversity in *Lampetra lethophaga* are consistent with the differentiation, seemingly mosaically arranged, that has been observed among lampreys in general, and among the nonparasitic forms in particular (Hubbs, 1925: 590). Some citations for the genus *Lampetra* are as follows: For subgenus *Entosphenus* — Creaser and Hubbs, 1922: 6, 10 – 11; Hubbs, 1925: 589; 1967. For subgenus *Lethenteron*

— Creaser and Hubbs, 1922: 12; Jordan and Hubbs, 1925: 98–99; Hubbs, 1925: 589; Berg, 1931: 92–93, 98–105; 1948: 35–42; 1962: 29–37; Hubbs and Lagler, 1958 and 1964: 36; Heard, 1966; Hubbs and Potter, in press. For subgenus *Lampetra* — Creaser and Hubbs, 1922: 13; Hubbs, 1925: 590. For all three subgenera — Hardisty, 1963: 20.

From a partial survey of the literature and from some original material I strongly suspect (see Hubbs and Potter, in press) that some of the rather confusing treatment of the local forms of *Eudontomyzon* reflect strong local diversity more complex than the simple alignment of the forms into two paired species, the parasitic *E. danfordi* Regan and the nonparasitic *E. vladykovi* (Zanandrea), plus the reputedly unpaired nonparasitic *E. mariae* (Berg).

A more detailed and more critical analysis and interpretation of the seemingly heterogeneous local populations of lampreys seems to be definitely in order.

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